



Universitat d'Alacant  
Universidad de Alicante

Comportamiento espacial y  
territorial del águila-azor  
perdicera *Aquila fasciata* y del  
águila real *Aquila chrysaetos* en  
el sudeste de España

Sara Teresa Morollón Ruiz



Tesis **Doctorales**

Unitat de Digitalització UA  
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Sara Morollón Ruiz

Tesis doctoral

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Universidad de Alicante

DEPARTAMENTO DE CIENCIAS AMBIENTALES Y RECURSOS NATURALES

FACULTAD DE CIENCIAS

UNIVERSIDAD DE ALICANTE

**Comportamiento espacial y territorial del águila-azor  
perdicera *Aquila fasciata* y del águila real *Aquila  
chrysaetos* en el sudeste de España**

**Sara Morollón Ruiz**

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**Dirigida por:**

**Prof. Dr. Vicente Urios Moliner**

**Dr. Pascual López López**



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*A mis padres*



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## SÍNTESIS GENERAL

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El estudio del uso del espacio y la territorialidad nos ayuda a tener herramientas para la conservación de especies. El territorio se ha definido de diferentes formas a lo largo de los años, se puede describir como el área defendida, el área dominada o el área de uso exclusivo entre otros. La territorialidad ofrece un lugar eficiente para satisfacer las necesidades básicas de alimentación, seguridad y reproducción. Las variaciones en los territorios de los animales pueden ser debidas a diferentes factores, como puede ser la densidad de población, la cantidad y calidad de los alimentos, las características del hábitat o los individuos que los ocupan. Estas variaciones se pueden estudiar de diferentes maneras: (i) tamaño y forma (capítulos 1, 2, 3 y 4); (ii) cambios estacionales (capítulos 1, 2 y 4); (iii) cambios anuales (capítulos 1, 3 y 4); (iv) cambios individuales (capítulos 1 y 4); (v) cambios respecto al éxito reproductivo (capítulo 1); (vi) cambios frente a una perturbación externa (capítulos 1 y 3).

En esta tesis se ha empleado una base de datos que lleva acumulando información satelital desde 2015. Cuenta con de más de 100 millones de localizaciones pertenecientes a 72 individuos de dos especies, águila-azor perdicera (56) y águila real (16), todos ellos marcados con dispositivos GPS/GSM.

La organización de la presente tesis se muestra a continuación, así como un breve resumen de cada uno de los capítulos que la componen, donde se destacan los hallazgos más relevantes.

**Capítulo 1:** Morollón, S., Urios, V., & López-López, P. (2022). Home-range size and space use of territorial Bonelli's Eagles (*Aquila fasciata*) tracked by high resolution GPS/GSM telemetry. *Diversity*. 14(12), 1082.

En este capítulo se investiga el uso del espacio del águila-azor perdicera a través del tamaño del área de distribución. Se analiza el papel del sexo, la temporada y el estado reproductivo. Estos análisis se han llevado a cabo a través de métodos de

densidad de kernel. En general, el tamaño del área de distribución de los individuos que ocupaban el mismo territorio es similar, principalmente debido al comportamiento de caza cooperativo exhibido por las diferentes parejas. No hay diferencias interanuales en el tamaño del área de distribución de la mayoría de los individuos, mostrando una fuerte fidelidad territorial de las parejas reproductoras. Debido a la disminución de la actividad en la temporada de reproducción a causa de la puesta, la incubación y la asistencia de los pollos en los nidos, el tamaño del área de distribución de las hembras es ligeramente menor que el de los machos. Los individuos territoriales no reproductivos muestran áreas de distribución mayores. La superposición entre territorios vecinos es muy baja y se evidencia un alto nivel de competencia intraespecífica en el águila-azor perdicera.

**Capítulo 2:** Morollón, S., Urios, V., & López-López, P. (2022). Fifteen days are enough to estimate home-range size in some long-lived resident eagles. *Journal of Ornithology*, 1-6.

En este capítulo se estudia la cantidad de localizaciones necesarias para que dos especies territoriales, águila-azor perdicera y águila real, definan su área de distribución. Se muestra que el número de localizaciones es independiente de la estación. Este objetivo es clave para los estudios de ecología espacial ya que la obtención de un gran conjunto de datos de animales marcados se vuelve difícil en términos económicos y logísticos. La dificultad para capturar y manejar individuos, la presión de trabajar con especies carismáticas y/o en peligro de extinción, y las limitaciones en el presupuesto financiero, hacen que muchas veces sea difícil trabajar con una gran cantidad de individuos. Además, en algunos casos, los transmisores dejan de emitir unos días después del marcado por diferentes motivos, incluida la mortalidad natural y no natural. En este apartado se muestra que después de un cierto número de días los individuos definen su territorio y mantienen su extensión y fisionomía.

**Capítulo 3:** Morollón, S., Pausas, J. G., Urios, V., & López-López, P. (2022). Wildfire response of GPS-tracked Bonelli's eagles in eastern Spain. *International Journal of Wildland Fire*, 31(9), 901-908.

En este capítulo se analiza por primera vez el comportamiento de un águila-azor perdicera frente a un incendio forestal, el cual quema la mayor parte del núcleo de su territorio, incluidas las zonas de roquedos donde se situaba el nido. Se observa un efecto negativo inmediato durante los primeros días del incendio forestal. El individuo se aleja en dirección contraria del área en llamas. Sin embargo, al cabo de unos días, el individuo recupera su comportamiento habitual. Durante los años consecutivos tiene el mismo área de distribución y se reproduce con normalidad. Esto podría ser el resultado de la adaptación de esta especie a los recurrentes incendios forestales en el área mediterránea.

**Capítulo 4:** Morollón, S., López-López, P. & Urios, V. (*en revisión*). A new view of territoriality. Design of protected areas with its application. *Ornithological Applications*.

En este capítulo se explora el conocimiento sobre territorialidad y uso del espacio del águila-azor perdicera. Se examina la plasticidad de los límites del territorio, la topografía y cómo se pueden modificar los territorios en función de sus ocupantes. Se analiza y se demuestra la similitud del área de distribución de individuos del mismo territorio, ya que sus límites no varían a lo largo del tiempo. Para ello se compara el porcentaje de superposición del área de distribución anual de los diferentes individuos que ocupan un territorio. Así mismo, los diferentes niveles de densidad de kernel y la excentricidad del territorio. Estas variables nos muestran que las diferentes áreas tienen la misma topografía y extensión. La invariabilidad se acentúa cuando, tras un reemplazo de uno o los dos individuos de la pareja se sigue manteniendo la topografía y extensión. Esto nos lleva a pensar que la identificación y conservación de los territorios de las grandes águilas, independientemente de sus habitantes y del estado de ocupación, es clave para asegurar la recuperación de las especies a largo plazo.



## INTRODUCCIÓN GENERAL

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La presente tesis aborda el comportamiento espacial y territorial del águila-azor perdicera y del águila real. Dos especies que son residentes en España y sus individuos ocupan un territorio durante todo el año.

El término *Territorio* lo definió Charles Moffat (1903), y años después Eliot Howard (1920) hizo la primera descripción sistemática de la función del territorio en la vida de las aves. Desde entonces se ha definido la territorialidad con diferentes criterios.

Con un punto de vista ecológico, definen la territorialidad como el *Uso exclusivo* de cualquier área ocupada. Este concepto se definió por el nivel de superposición de las áreas ocupadas por individuos o grupos (Maher y Lott, 1995).

Desde un punto de vista etológico, los territorios aportan una jerarquía de dominancia (Esser, 1971) y sirven entre otras cosas para canalizar y regular el comportamiento animal (Gold, 1982). Una definición es la *Defensa de un área*. Implica la defensa de un espacio limitado para restringir a otros animales, con agresiones y advertencias en los lindes del territorio (Maher y Lott, 1995). Originalmente, esta idea de territorialidad del área defendida se definió como la defensa del territorio por un macho contra otros machos de la misma especie (Kaufmann, 1983). Algunos autores definieron la territorialidad involucrando la defensa de un área fija (Brown, 1975; Kaufmann, 1983), mientras otros dicen que los territorios no necesariamente son fijos, sino que se defienden áreas móviles que pueden cambiar con el tiempo y el espacio (Wilson, 1975).

Otro enfoque según el comportamiento animal, es el *Dominio específico del sitio*. Se define el territorio como el área de distribución en la que un animal es dominante y agresivo contra los intrusos (Emlen, 1957). Esta definición discute la idea de exclusión y defensa del territorio y apoya la existencia de áreas superpuestas entre territorios vecinos con propietarios hostiles (Wittenberger, 1981).

El establecimiento de territorios por parte de animales, ya sea de forma permanente o temporal, brinda a muchas especies un medio eficiente para satisfacer sus necesidades básicas de alimentación, seguridad y reproducción (Gold, 1982). La rivalidad territorial normalmente se observa entre miembros de la misma especie, aunque hay casos de competencia entre especies estrechamente relacionadas (Orians y Willson, 1964). Las variaciones en los territorios pueden ser debidas a la densidad de población, la cantidad y calidad de los alimentos, las características del hábitat y los individuos que los habitan (Maher y Lott, 2000).

El conocimiento del área y la forma en que las especies ocupan los diferentes hábitats es de gran utilidad para defender y conservar los espacios donde se encuentran y por tanto también a las mismas especies.

Para tener herramientas en la conservación de las especies, en concreto las rapaces de larga vida residentes mediterráneas, águila-azor perdicera y águila real, debemos estudiar en profundidad las áreas de uso y de distribución de estas especies protegidas. Las variaciones en el área de distribución se pueden estudiar de diferentes maneras: (i) tamaño y forma; (ii) cambios estacionales; (iii) cambios anuales; (iv) cambios individuales; (v) cambios respecto al éxito reproductivo; (vi) cambios frente a una perturbación externa.

### **Especies de estudio**

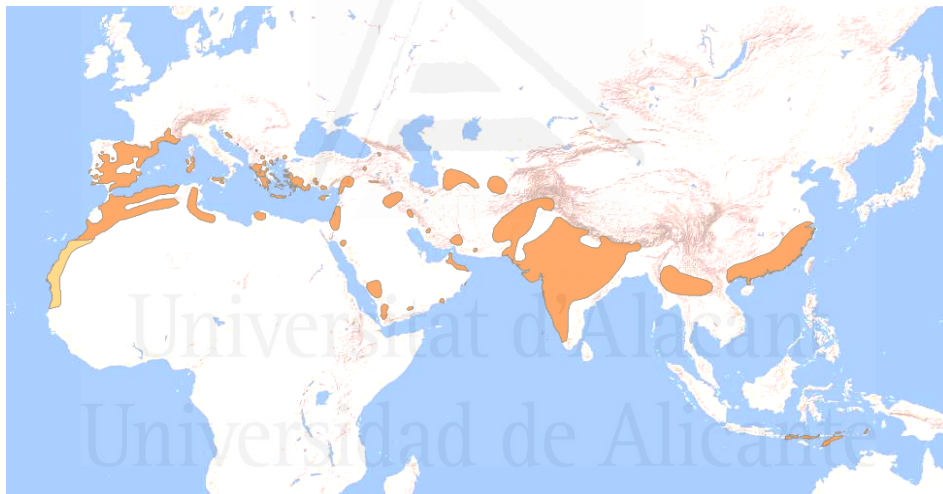
Las especies del género *Aquila* sp. son rapaces diurnas de mediano/gran tamaño. Tienen una silueta con un cuerpo compacto, cola larga en forma de abanico y alas largas y anchas para planear a bajo coste en las corrientes de aire. Tienen unas garras largas y afiladas que utilizan para matar y sujetar a sus presas y un pico grande y fuerte con el que desgarrarlas (Ferguson-Lees y Christie, 2001).

En la actualidad se reconocen 14 especies de águilas de este género, repartidas por todos los continentes, las cuales 4 de ellas son residentes en España. Estas especies son el águila imperial-ibérica (*Aquila adalberti*), águila calzada (*Aquila pennata*), águila real (*Aquila chrysaetos*) y águila-azor perdicera (*Aquila fasciata*).

Esta tesis se ha centrado en el águila-azor perdicera y en el águila real, dos especies que se caracterizan por su comportamiento estrictamente sedentario en España, ya que incluso los juveniles que suelen dispersarse y viajar muchos kilómetros de su zona de cría, se quedan dentro del país. Principalmente se ha estudiado el comportamiento territorial del águila-azor perdicera (Capítulos 1, 2, 3 y 4), y en menor medida, el del águila real (Capítulo 2).

### Águila-azor perdicera

El águila-azor perdicera es una rapaz diurna que se distribuye desde el sudeste asiático hasta la Península Ibérica y el Magreb (BirdLife International 2015; Figura 1). En España se encuentra en las sierras del este y sudoeste peninsular, con parches irregulares en el norte y en el centro (Del Moral y Molina, 2018).



**Figura 1** Distribución mundial del águila-azor perdicera. En naranja oscuro se observa la población residente y en naranja claro la población no reproductora (BirdLife International y Handbook of the Birds of the World, 2019).

Esta especie es estrictamente sedentaria en España, los ejemplares territoriales son monógamos y la pareja se asienta en un área de cría durante todo el año (Boch *et al.*, 2010). Es una especie fuertemente territorial y se observa una defensa del territorio cooperativa donde se suele ver a ambos miembros de la pareja volando y cazando juntos.



La población territorial del águila-azor perdicera se asienta en sierras o llanuras con una orografía abrupta con cortados rocosos. También seleccionan hábitats más abiertos o de baja cobertura vegetal como los matorrales, sabinars o cultivos arbóreos (Martínez *et al.*, 2014; SEO/BirdLife, 2021), zonas donde son más abundantes algunas de sus presas como conejos, liebres, palomas, córvidos y perdices (Gil-Sánchez *et al.*, 2004; López-López *et al.*, 2006; SEO/BirdLife, 2012). Estas zonas más abiertas son las zonas principales para la caza, tanto en los individuos territoriales como los de la población flotante (Mañosa *et al.*, 1998; Cadahía *et al.*, 2010).

Su alimentación se basa en mamíferos y aves de tamaño medio, como el conejo (*Oryctolagus cuniculus*), la perdiz roja (*Alectoris rufa*) o la grajilla (*Coloeus monedula*); y en menor medida, en reptiles, como el lagarto ocelado (*Timon nevadensis*) (Real *et al.*, 1996; Ferguson-Lees y Christie, 2001).

En las áreas de cría, normalmente el nido se sitúa en cortados rocosos desde pocos metros del suelo en pequeñas sierras, hasta a más de 100 metros de altura en acantilados de grandes macizos (Martí y Del Moral, 2003; Carrascal y Seoane, 2009; Bosch *et al.*, 2010). No obstante, algunas parejas sitúan los nidos en árboles (<8%; Del Moral y Molina, 2018) o en otras estructuras como en apoyos de tendidos eléctricos (<1%; Del Moral y Molina, 2018). En la región mediterránea, la puesta ocurre principalmente desde febrero hasta mediados de marzo (Orta *et al.*, 2013). El tamaño de ésta es normalmente de uno o dos huevos y muy ocasionalmente de tres (Arroyo *et al.*, 1995). La incubación de los huevos dura entre 37-41 días y se ocupa principalmente la hembra (Arroyo *et al.*, 1995). Los pollos permanecen en el nido entre 60-67 días (García, 1976; Arroyo *et al.*, 1976). En este periodo, su plumaje se ha desarrollado completamente aunque permanecen otros tres meses con los padres (Real *et al.*, 1998). Posteriormente hacen dispersiones de distancias variables entre 100 y 1.000 km del área de nacimiento (Cheylan *et al.*, 1996; Cheylan y Marmasse, 1998; Real and Mañosa, 2001) y se asientan temporalmente en las áreas de dispersión (Mañosa *et al.*, 1998). Éstas áreas se caracterizan por la ausencia de individuos territoriales y una gran abundancia de presas, destacando el conejo y la

perdiz roja (Mañosa *et al.*, 1998; Martí y Del Moral, 2003). La madurez sexual ocurre entre los 2-4 años en las hembras y 3-5 en los machos (Madroño *et al.*, 2004).

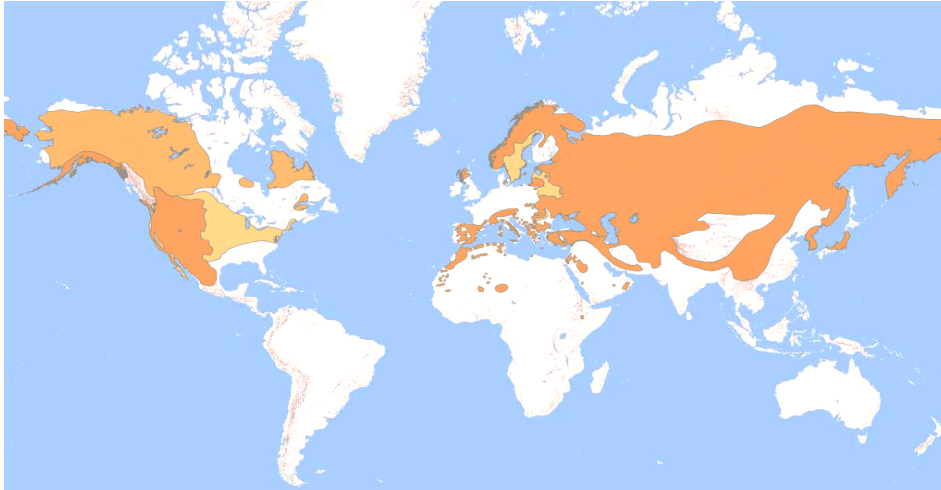
La población europea de águila-azor perdicera se estima en unas 1100-1200 parejas (BirdLife International, 2015), siendo la población española un 64%, con 711-745 parejas (Del Moral y Molina, 2018). En Europa, el tamaño de la población es actualmente estable, pero se estima que ha disminuido un 30% en tres generaciones (54 años) (BirdLife International, 2015). En España, en general se observa una tendencia negativa. El declive no ha sido homogéneo en todas las regiones, sino que varía del 28% en el litoral catalán al 80% en el norte peninsular. En algunos puntos del suroeste se observa cierta estabilidad (Del Moral y Molina, 2018). Es una especie clasificada según su estado de conservación como “Casi Amenazada” (Near Threatened; NT) en Europa (BirdLife International, 2015) y “Vulnerable” (VU) en España (SEO/BirdLife, 2021).

## Águila real

El águila real es una rapaz diurna con una distribución muy amplia. Se encuentra por todo el hemisferio norte donde las principales áreas de cría están entre los 70°N y los 20°N, no obstante hay alguna población en el norte de África y al sur de Etiopía (Figura 2).

En España, habita la subespecie *A.c. homeyeri* y ocupa los principales sistemas montañosos peninsulares, ausente especialmente en la meseta Norte, en la depresión del Guadalquivir, en la mayor parte de Galicia y en la costa del Cantábrico (Bautista, 2022).

Al igual que el águila-azor perdicera, el águila real en España es estrictamente sedentaria y los individuos territoriales se disponen en parejas ocupando un territorio durante todo el ciclo anual (Del Hoyo *et al.*, 1994; Ferguson-Lees y Christie, 2001).



**Figura 2** Distribución mundial del águila real. En naranja oscuro se observa la población residente y en naranja claro la población no reproductora (BirdLife International y Handbook of the Birds of the World, 2019).

Esta especie es más generalista respecto al hábitat que ocupa, tanto espacial como altitudinalmente (Bautista, 2022). Tiene preferencia por las zonas de montaña o serranía con paisajes abruptos y rocosos para la ubicación de los nidos (Watson, 1997; Martí y Del Moral, 2003; Bautista, 2022). No obstante, la gran plasticidad ecológica de esta especie (Watson, 1997), le permite ocupar paisajes abiertos como herbazales y matorrales o ambientes forestales como bosques de coníferas o de especies frondosas (Arroyo *et al.*, 1990; Fernández, 1993; López-López *et al.*, 2007).

Los ambientes más abiertos coinciden un con una mayor detectabilidad y disponibilidad de sus presas potenciales (principalmente perdices y conejos) (Soutullo *et al.*, 2008; Caro *et al.*, 2011). No obstante, su amplio espectro trófico permite que su dieta sea muy amplia, alimentándose de otras aves, mamíferos, reptiles, anfibios, peces, y carroña de forma variada, dependiendo de la disponibilidad regional de éstas (BirdLife International, 2021). Las presas capturadas suelen pesar entre 0,5 y 4,0 kg y la especie puede cazar en parejas o en pequeños grupos (Ferguson-Lees y Christie, 2001).

La nidificación se produce en zonas tranquilas con poca presencia humana, la altitud media del nido es de 950 m, con un rango entre los 160 m y los 2.150 m (Arroyo *et al.*, 1990; Del Hoyo *et al.*, 1994). La mayoría de los nidos se ubican en

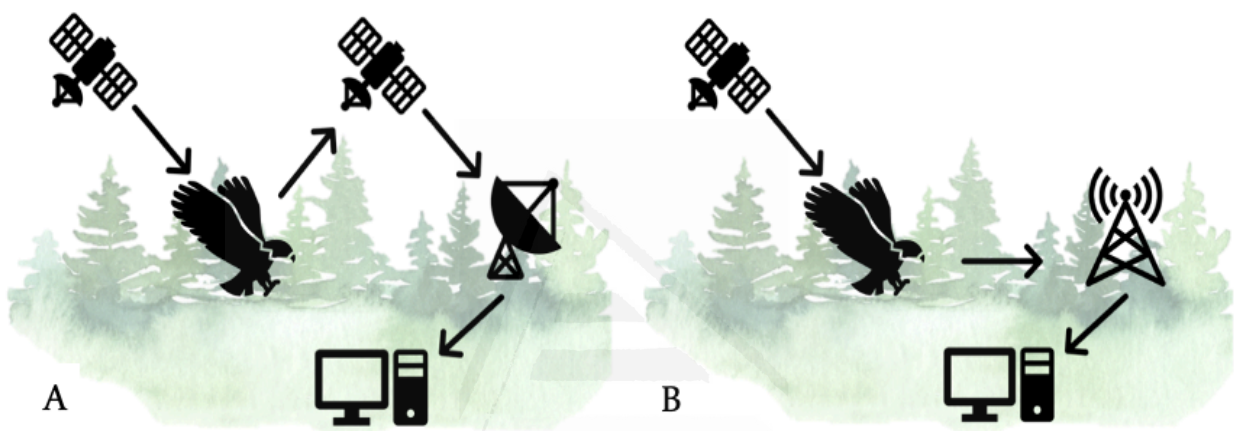
roquedos (90 %) y en menor cantidad en árboles (10%), principalmente grandes pinos, encinas o alcornoques (Martí y Del Moral, 2003). No obstante, en algunas zonas debido a la escasez de cortados rocosos, como en el valle del Ebro, el porcentaje de nidificación en árboles aumenta hasta un 40% (Madroño *et al.*, 2004). La puesta ocurre desde finales de febrero hasta finales de marzo y el tamaño medio de ésta es de 1,95 huevos, pudiendo variar entre uno y tres (Arroyo *et al.*, 1990). La incubación dura entre 41 y 45 días y los pollos desarrollan por completo su plumaje entre los 65 y 80 días, tras los cuales abandonan el nido (Madroño *et al.*, 2004). Sin embargo, los jóvenes dependen de los adultos durante tres meses más. Los individuos juveniles presentan un comportamiento dispersivo (Soutullo *et al.*, 2006a, 2006b) y ocupan áreas de asentamiento temporal que en ocasiones son compartidas con otras especies del género *Aquila* (Caro *et al.*, 2011).

La población europea estimada es de 9.300-12.800 parejas reproductoras (BirdLife International, 2021). España alberga una de las poblaciones más numerosas del continente, con s 1.752-1.915 parejas estimadas en el último censo de la especie (Bautista, 2022), siendo el 15-20% de la población europea. Entre las décadas de los 60' y 90', coincidiendo con la época de máxima persecución de las rapaces en España, su número de efectivos disminuyó un 30%. Desde entonces se ha recuperado la población, aumentando paulatinamente hasta las cifras actuales (Bautista, 2022). Este aumento supone un 49% en tres décadas desde el primer censo nacional en 1990 (Arroyo *et al.*, 1990). Según su estado de conservación se encuentra clasificada como “Menos Preocupante” (Least Concern: LC) en Europa (BirdLife International, 2021) y “Casi Amenazada” (Near Threatened; NT) en España (SEO/BirdLife, 2021).

### **Seguimiento de animales con telemetría satelital**

A finales de los ochenta se empezaron a utilizar los primeros dispositivos de telemetría satelital en estudios de movimiento animal a través de satélites Argos (Fancy *et al.*, 1988; Harris *et al.*, 1990). Los transmisores (Platform Transmitter Terminals; PTT) que se les coloca a los animales envían mensajes en frecuencias

especializadas a los satélites Argos que se sitúan en órbita baja. Los PTT modernos suelen tener también receptores de señales GPS (Global Positioning System) y envían ambas informaciones, GPS y Argos. Los mensajes se registran en los satélites y se remiten a centros de procesamiento situados en Estados Unidos y Francia. Las señales se procesan y los datos se mandan a los usuarios (Figura 3A). Debido al efecto Doppler (diferencia temporal entre la frecuencia recibida y emitida) que conlleva el uso de esta tecnología, las localizaciones podrían tener un error desde pocos metros a cientos de kilómetros (Douglas *et al.*, 2012).



**Figura 3** Movimiento de la señal según la técnica de telemetría satelital. (A) Telemetría GPS-Argos. (B) Telemetría GPS-GSM.

Hace casi dos décadas se empezaron a utilizar los primeros GPS con descarga de la información vía GSM (Global System for Mobile communication; Botha, 2006; Cordier, 2006; Figura 3B). Esta tecnología junto con el uso de baterías solares (las baterías convencionales eran muy pesadas) abrió un abanico de estudio de nuevas especies de animales. Los transmisores GSM ofrecen el potencial para una mayor cantidad de datos debido a su capacidad para registrar y transmitir datos GPS de alta frecuencia. Esto los hace excelentes para estudiar el uso del espacio a escala fina. Las localizaciones GPS se obtienen a intervalos que se correlacionan con el voltaje de la batería. Por tanto, se pueden adquirir posiciones de GPS con una mayor periodicidad con unas buenas condiciones de iluminación. Los datos recopilados incluyen ubicaciones GPS de alta resolución, debido principalmente a la gran velocidad de transmisión por vía GSM. Mientras que el transmisor esté

dentro del alcance de la red móvil y pueda establecer conexión, enviará datos instantáneamente. Los transmisores GPS/GSM archivan los datos (datalogger), por lo que si no se puede establecer una conexión, los datos se transmitirán una vez que el dispositivo pueda conectarse nuevamente a la red.

## **Base de datos**

En esta tesis se ha empleado una base de datos que lleva almacenando información satelital desde 2015, vinculada a diferentes proyectos de investigación (Tabla 1). Cuenta con más de 100 millones de localizaciones GPS de alta resolución, que corresponden a 72 individuos, siendo 56 águilas-azor perdiceras y 16 águilas reales.

Los individuos fueron capturados en su territorio con una red plegable activada por control remoto. La trampa estuvo bajo la vigilancia de los investigadores que estaban escondidos en los alrededores y fue activada tras comprobarse que los individuos objetivo estaban dentro. En la mayoría de los casos ambos miembros de la pareja de cada territorio, macho y hembra, quedaron atrapados juntos. Al detectarse un reemplazo en uno de los miembros de la pareja, el nuevo miembro fue capturado y marcado.

Los individuos se marcaron con datalogger GPS/GSM de batería solar, fabricados por e-obs GmbH (Munich, Alemania) y Ornitela (Vilnius, Lituania). El dispositivo fue colocado en la espalda con un arnés de teflón cosido con hilo de algodón para asegurar su desprendimiento tras un periodo de dos años aproximadamente. Los pesos de los transmisores fueron 48 y 50 g, respectivamente, y representaron el 1,66–2,86 % de la masa corporal de las águilas, por debajo del umbral del 3 % establecido para evitar efectos negativos en el comportamiento.

Las actividades de captura y marcaje fueron autorizadas y realizadas bajo permisos emitidos por las autoridades regionales (Conselleria de Agricultura, Medio Ambiente, Cambio climático y Desarrollo Rural, Generalitat Valenciana, España) y se hicieron todos los esfuerzos para minimizar el tiempo de manipulación para evitar cualquier sufrimiento a las águilas.

**Tabla 1** Proyectos de investigación vinculados a la base de datos de localizaciones GPS analizadas en esta tesis.

Nombre del proyecto	Fecha	IP	Entidad financiadora
Estudio de la incidencia real de la alimentación suplementaria sobre la ecología espacial y reproductora del águila-azor perdicera en la Comunidad Valenciana	01/05/2015-31/05/2021	Vicente Urios	Red Eléctrica de España
Solucionando problemas de conservación: análisis del riesgo de electrocución de especies amenazadas mediante telemetría satelital de alta resolución	01/09/2016-01/09/2017	Pascual López	Fundación Iberdrola España
Investigación aplicada a la conservación del águila perdicera en la Sierra de Espadán	05/02/2018-05/12/2018	Vicente Urios	Generalitat Valenciana
Seguimiento mediante telemetría satelital GPS/GSM de alta resolución de grandes águilas en la Comunidad Valenciana	25/10/2018-25/10/2021	Pascual López	ACCIONA Eólica de Levante
Seguimiento de grandes águilas en las Hoces del Cabriel y su entorno mediante telemetría GPS/GSM de alta resolución	25/01/2019-25/01/2022	Pascual López	LAFARGE Holcim
Investigación aplicada a la conservación del águila perdicera en el interior de Valencia	06/03/2019-06/09/2019	Pascual López	Generalitat Valenciana
Investigación aplicada a la conservación del águila perdicera en el interior de Valencia	16/04/2020-16/12/2020	Pascual López	Generalitat Valenciana
Marcaje y seguimiento de ejemplares de águilas	11/08/2020-11/08/2025	Pascual López	ACCIONA Eólica de Levante
Uso del espacio y análisis del comportamiento de grandes águilas en el entorno de infraestructuras de transporte de energía eléctrica	16/02/2021-16/02/2025	Pascual López	Red Eléctrica de España
Estudio cero: metodología y análisis del uso del espacio de grandes águilas en el entorno de los proyectos de energía solar fotovoltaica de Valle Solar en Ayora (Valencia)	01/07/2021-01/01/2022	Pascual López	SPV Genia Da Vinci
Estudio cero: metodología y análisis del uso del espacio de grandes águilas en el entorno de los proyectos de energía solar fotovoltaica de SOLAR ACAMAR REQUENA SLU, Valencia	13/08/2021-13/02/2022	Pascual López	Solar Acamar Requena
Seguimiento y conservación de grandes águilas en la Comunitat Valenciana	23/09/2021-23/05/2022	Pascual López	Generalitat Valenciana
Estudio cero: metodología y análisis del uso del espacio de grandes águilas en el entorno de los proyectos de energía solar fotovoltaica de Grenergy Renovables S.A. en Ayora (Valencia)	24/02/2022-24/08/2022	Pascual López	Grenergy Renovables
Captura, marcaje con emisores GPS y análisis del uso del espacio de dos parejas de águila perdicera en el entorno de la línea eléctrica a 400 kV La Plana-Morella	20/09/2022-20/09/2026	Pascual López	Red Eléctrica de España
Proyecto de investigación de ecología espacial de grandes águilas en relación con proyectos de restauración de canteras	14/11/2022-14/11/2025	Pascual López	LAFARGE Holcim
Efectos sinérgicos e impacto de energías renovables solar y eólica sobre la ecología espacial de grandes vertebrados mediante telemetría GPS/GSM de alta resolución	01/12/2022-30/11/2024	Pascual López	Ministerio de Ciencia e Innovación

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## **CAPÍTULO 1. Home-range size and space use of territorial Bonelli's Eagles (*Aquila fasciata*) tracked by high resolution GPS/GSM telemetry.**

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## Abstract

High-resolution GPS/GSM dataloggers provide spatial information of the highest quality, which outperform previous tracking methods such as ARGOS telemetry or conventional VHF ground-tracking. As a result, this has improved our knowledge of home-range behavior and spatial ecology of many species, including large raptors. In this paper, we use high-resolution GPS/GSM dataloggers to assess the home-range size and the role of sex, season (breeding or non-breeding season) and breeding status (reproductive or non-reproductive individuals) on space use of the Bonelli's eagle (*Aquila fasciata*). To this end, 51 territorial individuals (25 females and 26 males) were equipped with GPS/GSM transmitters and were tracked over 7 years (2015-2021) in eastern Spain. Overall, we recorded 4,791,080 fixes that were analyzed through kernel density methods (50%, 75% and 95% fixed kernels). The average individual home-range size according to the 95% kernel, 75% kernel and 50% kernel was  $54.84 \pm 20.78$  km<sup>2</sup>,  $24.30 \pm 10.18$  km<sup>2</sup> and  $11.17 \pm 4.90$  km<sup>2</sup>, respectively. Overall, the home-range size of individuals occupying the same territory was similar, mainly due to the cooperative hunting behavior exhibited by the species. We did not find interannual differences in the home-range size (95% fixed kernel) of most of the individuals, showing a strong territorial fidelity of the breeding pairs. In general, females' home-range size was slightly smaller than males' one due to the decrease of activity in the breeding season due to laying, incubation and chick attendance at nests. No seasonal variation in the 95% kernel was found, but there was in the 75% and 50% kernel. As of the breeding status, higher home-range size was recorded in the non-reproductive individuals. Moreover, we found low neighbor overlap among territories ( $4.18\% \pm 3.06\%$ ) that evidences a high level of intraspecific competition in Bonelli's eagles. Finally, this study highlights the advantages of the use of accurate telemetry information to improve our understanding of the spatial ecology of the endangered Bonelli's eagle, which ultimately will serve to better inform management actions for its conservation.

**Keywords:** animal behavior, birds of prey, datalogger, kernel density estimators, movement ecology, Spain.





## Introduction

The estimation of the home-range size and ranging behavior of predators is of great interest for their conservation, particularly of endangered species. This is the case of the Bonelli's eagle (*Aquila fasciata*), a long-lived medium-sized raptor classified as "Near Threatened" (NT) in Europe [1] and "Vulnerable" (VU) in Spain (RD 139/2011). This raptor has a large worldwide distribution, from the Iberian peninsula to Southeast Asian [2]. In Spain, this species usually occupies Mediterranean habitats with evergreen forest and an abrupt orography where it found adequate places for nesting in cliffs and occasionally on trees. The Bonelli's eagle shows a strongly territorial behavior, defending its territory in pairs, where both individuals remain usually together [3–6]. Previous research about the home-range size and ranging behavior of the Bonelli's eagle were mostly based on radio-tracking technology [7] or based on GPS-Argos telemetry [8,9]. Recently, the use of GPS/GSM dataloggers is allowing a large number of precise locations per day, thus favoring the advance of our understanding of the species' ecology.

This study provides a detailed assessment of space use and home-range size of territorial Bonelli's eagle in Mediterranean landscapes. In addition, we further explored the role of sex, seasonal variations, breeding status, and the neighbor competitive pressure, on home-range size. This is the first time that this information has been assessed with high-resolution GPS/GSM technology incorporating the highest accuracy. Thus, this investigation provides new information on the spatial ecology of the species taking advantage of a larger sample size in terms of individuals and number of locations in comparison to previous works. Hence, the main goals of this study are: (i) to describe the home-range size and ranging behavior of territorial Bonelli's eagles; (ii) to examine the influence of sex, season (breeding/non-breeding season) and breeding status (reproductive/non-reproductive individuals) in spatial ecology; and (iii) to assess the territorial interaction between neighboring individuals.

## Materials and Methods

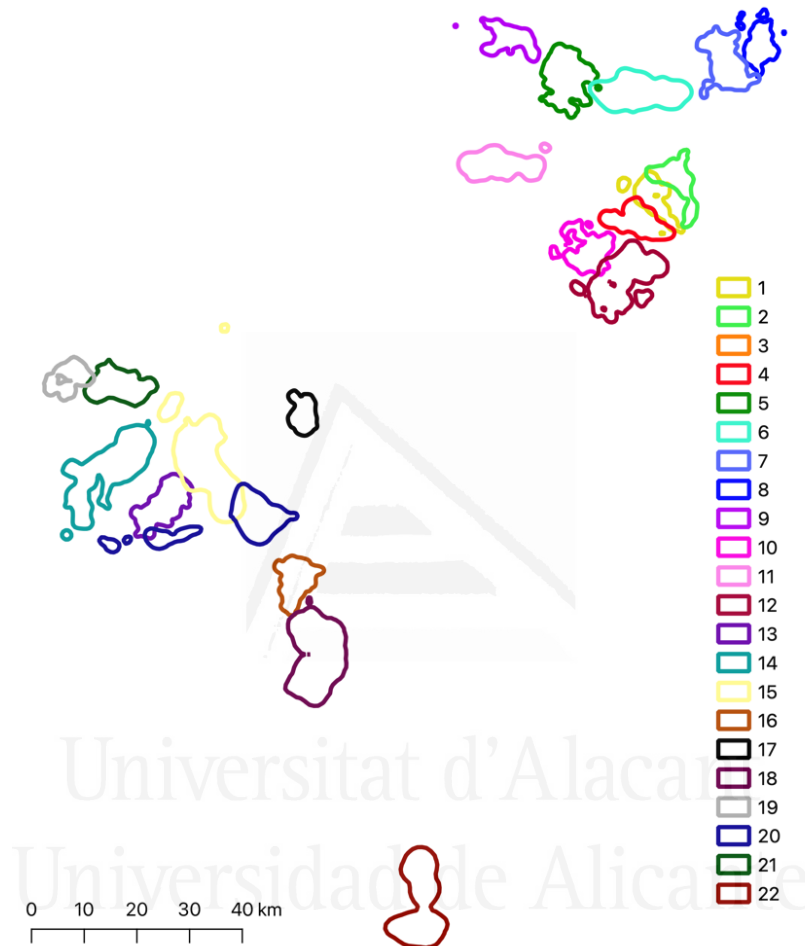
### Study area

The study area is located in eastern Spain including Albacete, Alicante, Castellón, Cuenca and Valencia provinces. The area covers approximately 7,600 km<sup>2</sup> with an average altitude ranging between the coastline and 1,200 m asl. The climate is Mediterranean with an average annual temperature that varies between 17°C in the coastal areas and 8°C in the inner mountains. The dominant landscape is composed by Mediterranean scrublands (*Pistacia lentiscus*, *Rosmarinus officinalis*, *Thymus vulgaris*, *Stipa tenacissima*), oak forests (*Quercus ilex*, *Q. faginea*, *Q. suber*) and Mediterranean evergreen forests (*Pinus halepensis*, *P. pinaster*, *P. nigra*).

### Tracking

A total of 51 territorial adult and subadult Bonelli's eagles, 26 males and 25 females, were trapped in 22 different territories (Figure 1) by means of a remotely activated folding net between 2015 and 2021 (see Table S1, in Supplementary Material). The trap was always under surveillance of the researchers which were hidden in the nearby. The trap was only activated once checked the target individuals were inside. Both pair members of each territory, male and female, were trapped together in most cases. When a turnover in one of the pair members was detected (usually after the death of the former member), we trapped and marked the new member. All individuals were tagged with GPS/GSM solar energy dataloggers manufactured by e-obs GmbH (Munich, Germany) and Ornitela (Vilnius, Lithuania) using a backpack configuration by means of a Teflon tubular harness designed to ensure that the harness fell off at the end of the tag's life. The weight of the transmitters was 48 and 50 g, respectively, and represented 1.66 to 2.86% (average = 2.25%, SD = 0.38%) of the body mass of eagles, below the 3% threshold established to avoid negative effects on behavior [10,11]. The duty cycle of the transmitters was programmed to record a GPS location at five-minute

intervals [4,5], from 1 h before sunrise to 1 h after sunset, year-round. Moreover, transmitters recorded one fix per hour during nighttime. Transmitters' data was retrieved, stored and managed by means of the Movebank online repository (<http://www.movebank.org/>).



**Figure 1** Spatial arrangement of 22 Bonelli's eagle territories in the study area. Due to conservation reasons, the map is blind to avoid the exact location of each territory.

### Ethic statement

Trapping and marking activities were authorized and conducted under permissions issued by regional authorities (Generalitat Valenciana and Junta de Comunidades de Castilla-La Mancha, Spain) and all efforts were made to minimize handling time to avoid any suffering to eagles.

## Home-range analysis

We used kernel density estimation (KDE) methods [12] to compute home-range size using the "reproducible home-range" (*rhr*) R package [13,14]. The KDE methods are widely used to calculate home-range size in different taxonomic groups such as in fishes (e.g. [15]), reptiles (e.g. [16]), mammals (e.g. [17–22]) and birds (e.g., [4,5,23–28]). We preferably used KDE instead of autocorrelated KDE (AKDE) methods because in our experience, computations based on AKDE methods result in unrealistic larger home-range size (debated in [29]).

We considered three kernel levels: the 50% kernel (K50% isopleth) that is the nuclear area of the home-range, where the nest is usually located; the 75% kernel (K75% isopleth) which was considered as the intermediate area of active use, which includes the feeding and resting areas; and the 95% kernel (K95% isopleth) that was considered as the total area of the home-range [30,31]). We used the daily individual K50%, K75% and K95% isopleths computed with the whole tracked period from the following day after tagging to the end day of data transmission (e.g. animal's death, end of transmission), knowing that 15 days is the minimum tracking period to obtain a complete home-range [5]).

## Data modelling

Overall, we recorded 4,791,080 high precision GPS location of the 51 adult Bonelli's eagles (26 males and 25 females) tracked during the period 2015-2021.

We used Generalized Linear Mixed Models (GLMM; [32]) to analyze the variation of the monthly average of daily home-range size within each territory, considering "Territory" and "Individual" as random factors. "Individual" was nested into "Territory" to account for the hierarchical structure (i.e., non-independence) of data [33]). The variation in home-range size was examined in relation to three fixed binary factors: "Sex", "Breeding" and "Season". We consider "Breeding" as the annual breeding status of the pairs, taking into account the years in which each pair did reproduce ("Yes") and those in which they did not ("No"). "Season" was

determined by using individuals' data combining fieldwork observations and detailed tracking information, and was divided into two different periods: breeding season and non-breeding season. The “Breeding season” was considered from January to June (since all pairs breed within these months) and the “Non-breeding season” from July to December. The monthly average of daily home-range sizes according to the three different spatial estimators (K95%, K75% and K50%) were logarithmically transformed and were used as the response variable in the GLMMs. The R package used for the analyses was “*lme4*” [34].

We used a one-way ANOVA test to analyze the interannual differences in the monthly average of daily home ranges (95% kernel) of the individuals occupying the same territory in different years (i.e., individuals tracked for at least two years).

Finally, we calculated the annual territorial overlap between the individuals who occupy simultaneously (i.e., in the same year) neighboring territories. The annual percentage of overlap between neighboring territories was compared using the 95% kernel under the “*raster*” R package [35].

## Results

### Individual home-range size

The average K95%, K75% and K50% were  $54.86 \pm 20.57 \text{ km}^2$  (range: 22.44 - 116.11  $\text{km}^2$ ),  $23.91 \pm 10.47 \text{ km}^2$  (range: 10.14 - 56.42  $\text{km}^2$ ), and  $11.17 \pm 4.86 \text{ km}^2$  (range: 4.59 - 27.32  $\text{km}^2$ ), respectively (Figure S1 and Table S2 in Supp. Mat.).

### Differences in home-range size

Our results showed that home-range size can be explained by the additive effects of “Sex”, “Breeding” and “Season” as well as the interactions between “Sex”

**Table 1** Generalized Linear Mixed Model (GLMMs) results of variation in home-range size using three different spatial estimators. Significant values are in bold.

Variable	Indep. Variable	Estimate	SE	t	d.f	p-Value
K95%	(Intercept)	3.817	0.071	53.729	20.727	<0.001
	Sex (Female)	-0.084	0.023	-3.608	24.589	<b>0.001</b>
	Breeding (No)	0.042	0.019	2.179	1234.838	<b>0.030</b>
	Season (Breeding)	-0.016	0.017	-0.899	1221.358	0.369
	Sex (Female)*Breeding (No)	0.017	0.018	0.948	707.351	0.343
	Sex (Female)*Season (Breeding)	-0.048	0.017	-2.761	1222.184	<b>0.006</b>
	Breeding (No)*Season (Breeding)	0.094	0.018	5.373	1232.930	<0.001
	Sex (Female)*Breeding (No)*Season (Breeding)	0.011	0.017	0.616	1226.767	0.538
K75%	(Intercept)	2.974	0.076	39.063	20.855	<0.001
	Sex (Female)	-0.100	0.025	-3.906	24.274	<b>0.001</b>
	Breeding (No)	0.057	0.020	2.851	1237.418	<b>0.004</b>
	Season (Breeding)	-0.045	0.018	-2.513	1220.620	<b>0.012</b>
	Sex (Female)*Breeding (No)	0.026	0.019	1.349	753.480	0.178
	Sex (Female)*Season (Breeding)	-0.059	0.018	-3.274	1221.557	<b>0.001</b>
	Breeding (No)*Season (Breeding)	0.107	0.018	5.823	1232.456	<0.001
	Sex (Female)*Breeding (No)*Season (Breeding)	0.017	0.018	0.957	1227.514	0.339
K50%	(Intercept)	2.180	0.078	28.047	20.908	<0.001
	Sex (Female)	-0.106	0.027	-4.012	24.016	<b>0.001</b>
	Breeding (No)	0.067	0.020	3.313	1238.865	<b>0.001</b>
	Season (Breeding)	-0.063	0.018	-3.422	1220.088	<b>0.001</b>
	Sex (Female)*Breeding (No)	0.028	0.019	1.467	781.441	0.143
	Sex (Female)*Season (Breeding)	-0.063	0.018	-3.440	1221.091	<b>0.001</b>
	Breeding (No)*Season (Breeding)	0.116	0.019	6.252	1232.181	<0.001
	Sex (Female)*Breeding (No)*Season (Breeding)	0.019	0.018	1.055	1227.970	0.292

and “Season” and “Breeding” and “Season”. The interaction between “Sex” and “Breeding” was not significant across the three different spatial estimators. The multiple interactions between the three effects was not significant across the three spatial estimators (K95%, K75% and K50%) (Table 1). Results of  $R^2_{\text{conditional}}$  corresponding to the effect of combined fixed and random factors were 0.259, 0.282 and 0.295 according to K95%, K75% and K50%, respectively. The variance explained by random factors (obtained as  $R^2_{\text{conditional}} - R^2_{\text{marginal}}$ ) was 0.217, 0.226

and 0.228 according to K95%, K75% and K50%, respectively. In general, taking into account all individuals, the home-range size (K95%, K75% and K50%) was larger in males than in females ( $p < 0.001$  in all cases), also larger during the non-breeding season (only K75% with  $p = 0.012$  and K50% with  $p = 0.001$ ) and in the years that the pair did not breed ( $p = 0.030$ ;  $p = 0.004$ ; and  $p = 0.001$ , respectively) (Table 1).

Taking into account the Season and the Sex, females showed a monthly average daily home-range size smaller than males during the breeding season, (Table 1, Table 2 and Figure 2). In contrast, there were no differences in home-range size during the non-breeding season (Table 1, Table 2 and Figure 2).

**Table 2** Monthly average ( $\pm$  standard deviation) daily home-range size (km<sup>2</sup>) of the three levels (K95%, K75% and K50%) taking into account “Season”, “Sex” and “Breeding Status”.

Season	Sex	Breeding Status	n	K95%	K75%	K50%
Breeding	Females	-	283	48.30 $\pm$ 30.60	20.60 $\pm$ 14.40	9.21 $\pm$ 6.65
Breeding	Males	-	319	62.80 $\pm$ 46.70	27.40 $\pm$ 22.60	12.40 $\pm$ 10.80
Non-Breeding	Females	-	318	56.20 $\pm$ 35.30	25.30 $\pm$ 17.30	11.70 $\pm$ 8.30
Non-Breeding	Males	-	337	57.20 $\pm$ 29.80	25.60 $\pm$ 13.90	11.80 $\pm$ 6.62
Breeding	-	No	270	61.50 $\pm$ 35.60	26.90 $\pm$ 17.00	12.30 $\pm$ 8.13
Breeding	-	Yes	332	51.60 $\pm$ 43.70	22.10 $\pm$ 21.10	9.77 $\pm$ 9.90
Non-Breeding	-	No	288	51.40 $\pm$ 32.10	23.20 $\pm$ 15.30	10.70 $\pm$ 7.28
Non-Breeding	-	Yes	367	60.80 $\pm$ 32.40	27.20 $\pm$ 15.60	12.50 $\pm$ 7.54

Taking into account the Season and the Breeding Status, non-reproductive individuals showed a monthly average daily home-range size larger than reproductive individuals during the breeding season, (Table 1, Table 2 and Figure 2). During the non-breeding season, the reproductive individuals showed a monthly average daily home-range size larger than non-reproductive individuals (Table 1, Table 2 and Figure 2). More detailed comparisons are available in Supplementary Material (Figures S2 – S12).

Our results show an inflection point in the monthly home-range size pattern in June and December, both when comparing sexes and breeding status.



Females increase their home-range in June and it is similar to that of males until December when it decreases again. Regarding the breeding status, breeding individuals increase their home-range in June and decrease in December, while the opposite happens for non-breeding individuals (Figure 2).

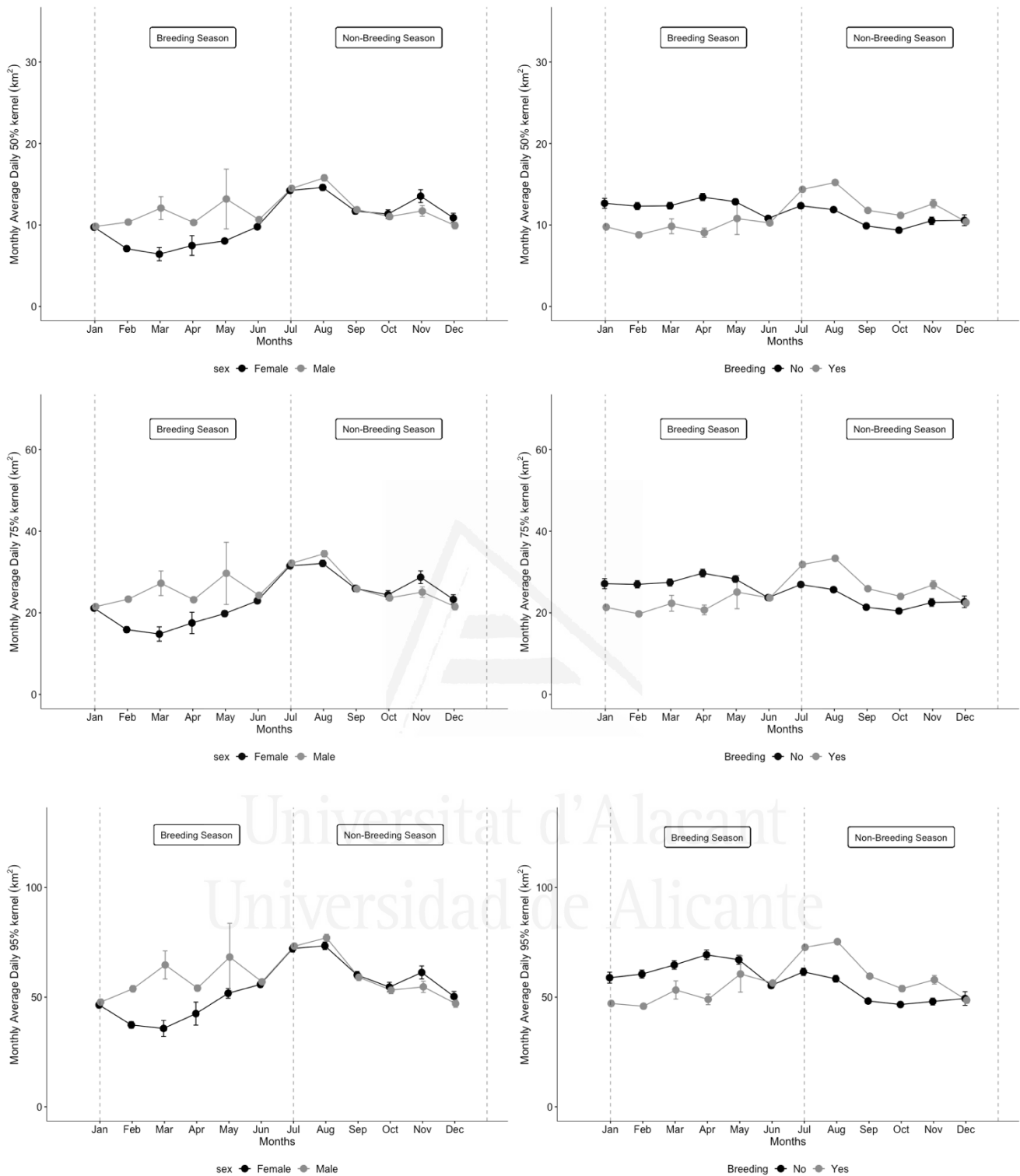
There were no interannual differences in the monthly average of daily home range size according to the 95% kernel in the most part of the individuals which were tracked two years or more (68.18%, n = 44) (Table S3 in Supp. Mat.).

### Overlapping between neighboring territories

The overlap between neighbors home-ranges (K95%) of all individuals (n=38) showed an average value of  $4.18 \pm 5.53$  % (Table 3). There were five territories (territories number 9, 11, 14, 17 and 22) that were not used in this analysis because they had no neighboring territories occupied in the same year or because there were isolated.

**Table 3** Average and standard deviations (SD) of overlap percentages between simultaneous neighboring territories.

Territory 1 (T1)	Territory 2 (T2)	Average overlap % T1-T2	SD overlap % T1-T2	Average overlap % T2-T1	SD overlap % T2-T1
1	2	3.71	3.76	3.60	3.14
1	3	0.15	NA	0.07	NA
1	4	9.95	1.85	10.71	2.19
1	12	0.49	NA	0.30	NA
2	3	2.67	3.21	1.66	2.30
6	3	5.23	3.86	3.98	3.05
8	7	0.72	0.33	0.45	0.24
10	12	0.72	0.33	1.96	0.85
15	13	1.12	0.52	2.76	1.70
15	20	19.74	12.03	9.30	3.06
16	18	1.09	1.24	0.55	0.61
20	13	4.68	2.43	20.17	19.18
21	19	1.19	0.51	1.70	0.87
<b>Total</b>				<b>4.18</b>	<b>5.53</b>



**Figure 2** Seasonal differences between sexes (left) and breeding status (right) in the monthly average of daily home-range size (K95%, K75% and K50%) over the year. Vertical dashed black lines delimitate the different seasons.

## Discussion

Our results show that Bonelli's eagles extend their home-range  $54.84 \pm 20.78$  km<sup>2</sup>, which ranges between 22 and 116 km<sup>2</sup> according to the 95% kernel. These results are larger than those described by [36] in Valencia (30.5 km<sup>2</sup>, range: 15.82–44.48 km<sup>2</sup>) and those of [7] in Catalonia (36.1 km<sup>2</sup>; range: 33.4–110.7 km<sup>2</sup>) both using radio-tracking techniques. In contrast, our results are similar to those reported by [8] in Valencia and Tarragona ( $44.4 \pm 15.4$  km<sup>2</sup>; range: 31.8–91.9 km<sup>2</sup>) and [9] in Aragón, both of them using GPS-Argos telemetry (57.25 km<sup>2</sup>; range: 23.48–152.24 km<sup>2</sup>). The higher accuracy of GPS locations in comparison to VHF radio-tracking accounts for the differences observed between methods [37].

The high variability in the home-range size across territories may be due to different factors, such as geographical differences [38], the pressure from neighboring pairs, population density [3,39], interactions with humans [23] and/or the different quality of territories [40]. This indicates that there might be territories with high availability of prey that allow pairs to survive for years, while others can be up to three or four times larger.

### Differences in home-range size between sexes and seasons

Overall, males showed larger home-range size than females. However, these sex differences were not previously described in the literature [7–9,36]. Sexual differences could be explained by the decrease in the home-range size of the females during the breeding season because they move less since they are in charge of the incubation and chicks' attendance [4]. This decrease in this period affects the general size of females' home-range. In contrast, during the breeding period, males are in charge of prospecting the home-range for hunting and delivering the prey to the nest to feed the female and the chicks [4].

In contrast to previous studies, we found no differences in home-range size between the breeding and non-breeding season, at least according to the K95%. For example, some studies reported larger home-range in the breeding season [8],

whereas others in the non-breeding season [7,9]. These differences could be accounted for the different quality of information since our data are based on a larger sample size ( $n = 51$ ) and higher accuracy (GPS/GSM technology versus radio-tracking or Argos-GPS information).

Furthermore, when “Season” and “Sex” were taken into account at the same time, we detected a smaller home-range size of females in the breeding season due to the lesser movement during the incubation and chicks' attendance. However, during the non-breeding season, no differences were found between males and females in their home-range. This could be explained since they spend most of their time together according to GPS information and direct observation in the field (i.e., resting, cooperative hunting, flying, etc.).

### **Differences in home-range size between breeding status and seasons**

The inflection point in territory size observed in June (Figure 2), where breeding individuals increase their home-range, coincides with the abandonment of the nest by juveniles. Once the juveniles are more independent, relaxation and less parental effort take place, and thus an increase in their home-range is observed. On the other hand, non-breeding individuals keep their territory constant throughout the year. Our results show that the home-range of breeding individuals increases whereas those of non-breeding individuals decrease. This can be explained since breeding pairs are the ones that set the tone as they have more energy requirements and are presumably in better physical shape. In contrast, the non-breeding pairs are the ones that need to adjust to these requirements, occupying or ceding territory depending on the breeding pairs. This inflection point is also seen in December, where the opposite occurs, increasing the breeding area in non-breeding individuals and decreasing in the breeding ones.

### **Overlap between neighboring territories**

We observed a low overlap of home-ranges between neighbors. This could be explained by the high level of intraspecific competition of the Bonelli's eagle.

The consistency of our results (4.18%) with previous studies is remarkable (4.1% in [7]; 4.33% in [8]). Bonelli's eagles are territorial raptors that exhibit agonistic behavior in case of territorial invasion and they even extend their territory in case of disappearance of a neighboring pair (authors' pers. obs.)

### **Implications for conservation**

The information provided in this study on the home-range size and ranging behavior of the Bonelli's eagle throughout the annual cycle provides a useful tool for the management and conservation of this species. The Bonelli's eagle is one of the key species used to delimitate protected areas in Mediterranean ecosystems. Thus, a detailed knowledge of the home-range size and its variation throughout the annual cycle could be used to design them much more effectively. This information will also make possible to assess the impacts of various anthropic activities and to mitigate or even eliminate them. In contrast to the general pattern used decades ago, in which land planning was focused only in protecting nesting areas and the immediate nearby, our study shows that the continued presence of pairs throughout its territory all over the year (see K95%, K75% and K50%) requires a comprehensive protection or management of the entire home-range, including not only nesting areas but also feeding and resting grounds.

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## **CAPÍTULO 2. Fifteen days are enough to estimate home-range size in some long-lived resident eagles.**

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## Abstract

In this paper, we show how many fixes are enough to define the territory of two long-lived resident raptors marked by GPS transmitters. To this end, we analyzed high-resolution GPS data from 50 territorial Bonelli's eagles (*Aquila fasciata*) and 9 territorial Golden eagles (*Aquila chrysaetos*) equipped with GPS/GSM dataloggers. Our results show that between 2200 and 2800 fixes are enough to define the territory. This is interesting for movement ecology works where long-term GPS data series are not available.

**Keywords:** *Aquila fasciata* · *Aquila chrysaetos* · Accumulation curve · Breakpoint regression · GPS · Kernel density · Telemetry · Territory



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## Introduction

Movement ecology has emerged as a transdisciplinary discipline with an exponential increase of studies including many different taxa worldwide (Nathan et al. 2008; Kays et al., 2015; Tucker et al. 2018). Estimating how many locations are needed for territorial species to define their home range is key for spatial ecology studies, particularly of long-lived resident raptors, for which obtaining a large dataset of marked animals becomes difficult in economic and logistical terms. Difficulty in capturing and handling individuals, the pressure of working with charismatic and/or endangered species, and the limitations in financial budget, particularly in countries of the global South, among others, make often difficult to work with a large amount of individuals. In addition, in some cases, transmitters stop emitting a few days after tagging for different reasons including natural and unnatural mortality. After almost 20 years of experience with large eagles tracked by different telemetry technologies (i.e., radio-tracking, Argos satellite, GPS and current GPS/GSM telemetry), we have observed that after a certain number of days eagles of both sexes define their territory and maintain its extension and topology with little variation in successive years.

## Materials and Methods

The study area is located in eastern Spain including Albacete, Alicante, Castellón, Cuenca and Valencia provinces. The area covers approximately 8000 km<sup>2</sup> with an average altitude ranging from 100 to 1500 m above sea level. The climate is Mediterranean with an average annual temperature varying between 17 °C in the coastal areas and 8 °C in the inland mountains. The dominant landscape is composed by Mediterranean evergreen forests (*Pinus halepensis*, *P. nigra*), oak forests (*Quercus rotundifolia*, *Q. suber*) and Mediterranean scrublands.

In this study, we used a current dataset of 50 adult and subadult Bonelli's eagles (*Aquila fasciata*), 25 males and 25 females, and 9 adult Golden eagles (*Aquila*

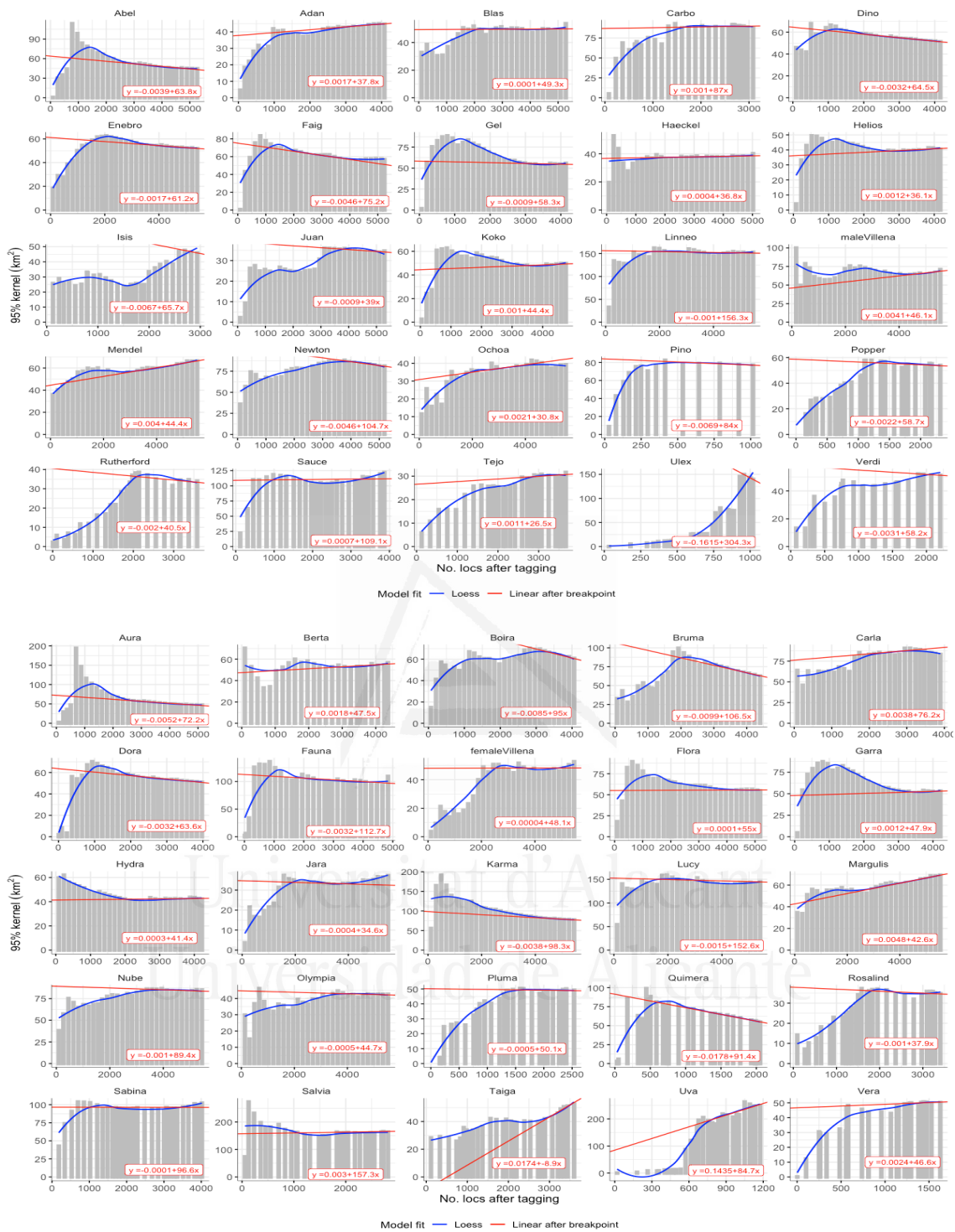
*chrysaetos*), 5 males and 4 females. All the individuals were captured and tagged in their territory with GPS/ GSM solar energy dataloggers manufactured by e-obs GmbH (Munich, Germany) and Ornitela (Vilnius, Lithuania) using a backpack configuration. Transmitters weights were 48 and 50 g, respectively, and represented 1.66–2.86% (mean = 2.25%, SD = 0.38%) of the eagles' body mass, below the 3% threshold established to avoid negative effects on behavior (Kenward 2001; García et al. 2021). Tagging details are available in detail in Perona et al. (2019). Trapping and tagging activities were authorized and conducted under permissions issued by regional authorities (Conselleria de Agricultura, Medio Ambiente, Cambio climático y Desarrollo Rural, Generalitat Valenciana, Spain) and all efforts were made to minimize handling time to avoid any suffering to eagles. Transmitters were programmed to obtain GPS fixes with a sampling frequency of five minutes during daytime (e.g., LópezLópez et al. 2021). All eagles were territorial according to field observations and GPS information.

To determine the amount of GPS fixes or days needed to delimit and define an individual's territory, homerange indicators were computed using kernel density methods (KDE) (Worton 1989). For this, we obtained the 95% daily accumulative kernel (K95%) from the day of tagging to the 30th day of data transmission using the “reproducible home-range” (*rhr*) R package (Signer and Balkenhol 2015). The 95% kernel was considered as the home-range area (Samuel et al. 1985) and is the most common metric in spatial ecology studies for homerange delineation within territories. Kernel surface tends to increase from the first GPS locations after tagging until the animal delineates its home-range area. Mathematically, this results in an asymptote of the daily K95% accumulation curve. To check this, we plotted the K95% area versus the number of accumulation fixes, and also the K95% area versus time. Since there is a non-linear relationship between both variables, we computed data breakpoints to assess when the home-range size has already been fully defined. Breakpoints were calculated using the piecewise regression method (Neter et al. 1985; Toms and Lesperance 2003) implemented in the “*segmented*” R package (Muggeo 2017). This method splits the

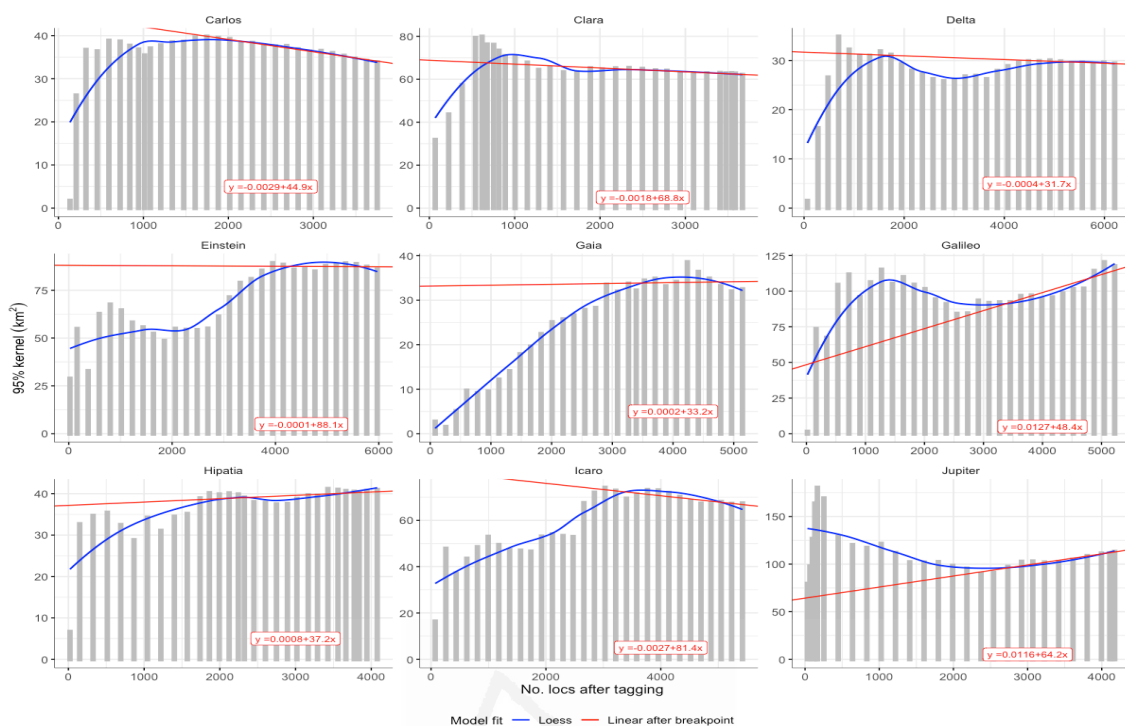
independent variable (i.e., number of locations or number of days after tagging) into different intervals with different slopes calculating separate line segments that fit to each interval. A linear model was calculated using the data after the last breakpoint to determine when there is no increase in the home-range area (i.e., when the slope tends to zero). The breakpoints were used to estimate when eagles had reached the asymptote and thus when they had delimited their home range. We also repeated this analysis using monthly and seasonal data (i.e., breeding and non-breeding seasons) to check if the general pattern of stabilization of the home-range size after a given number of locations or time period is consistent. To this end, we verified it with six individuals with the longest tracking time redoing the analyses instead from the first day after tagging, by taking data month by month and by breeding and non-breeding season. Differences in the number of fixes per month and/or period were tested by means of a one-way ANOVA and a post hoc Tukey test (Figures and data in Supplementary Material). Finally, to test if there are differences in the number of locations between species and sexes (only in Bonelli's eagle because the data are representative enough), a one-way ANOVA was performed. Statistical significance was set at  $P < 0.05$ .

## Results

Our results showed that the mean minimum number of fixes to define the territory was  $2209 \pm 538$  and  $2795 \pm 50$  fixes in the Bonelli's eagle and the Golden eagle, respectively, and in our case, it corresponds to  $15.64 \pm 6.74$  and  $13.72 \pm 4.98$  days. The mean slope of the linear model after the data breakpoint of all individuals was  $0.008 \pm 0.028$  ( $0.495 \pm 0.523$  for minimum number of days) (Figures 1, 2). There were neither differences in the number of locations between species ( $F = 2.746$ ;  $p = 0.103$ ) nor between sexes in Bonelli's eagle ( $F = 0.037$ ;  $p = 0.849$ ).



**Figure 1** Accumulation daily 95% kernel surface of Bonelli's eagle tracked with GPS/GSM transmitters by the accumulation number of fixes during the first 30 days after tagging. Linear regression fit after the breakpoint (red line) and smoothed fitting line (blue line) are shown. **A** for 25 females **B** for 25 males. Linear regression fit after the breakpoint (red line) and smoothed fitting line (blue line) are shown



**Figure 2** Accumulation daily 95% kernel surface of 9 Golden eagles tracked with GPS/GSM transmitters by the accumulation number of fixes during the first 30 days after tagging. Linear regression fit after the breakpoint (red line) and smoothed fitting line (blue line) are shown

## Discussion

According to our results, we propose that in studies with long-lived resident raptors, we can consider that between 2200 and 2800 fixes after tagging would be enough to define the extent of their home range based on the 95% kernel. In fact, this is a common metric used in movement ecology studies and, in contrast to other more sophisticated metrics, is easily calculated by researchers and specialists that use GPS telemetry.

Since no differences were found between species, it would be interesting to check whether these results could be extrapolated to other similar long-lived resident eagles. We hypothesize that this could be true taking into account that long-lived raptors need to fly over their entire territory in a few days both to

hunting and to defend it from other territorial pairs in the neighborhood. Regarding the absence of sex differences in Bonelli's eagle home ranges, this is to be expected due to the cooperative hunting behavior typical of this species.

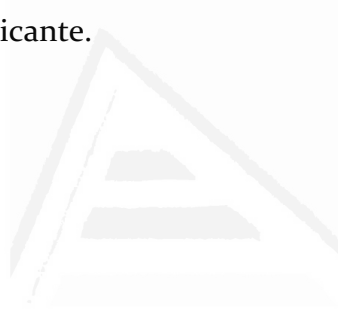
Our results can be extrapolated to other large eagles that have a similar hunting behavior to the Golden eagle and the Bonelli's eagle, which explore their territories from the air to attack their prey. Since our data sampling frequency is very high (one location every five minutes) and that these two species have a continuous flight, the number of locations needed to define the home-range size is achieved in just 15 days. In the case of slower species or for species sampled with lower time resolution, the lower number of locations would be compensated by the larger territory covered by them.

The capture and tagging of individuals is carried out outside the breeding season so as not to interfere with the breeding season. For this reason, we do not consider the 15-day period of total exploration of the home range for breeding individuals, as during the breeding season, long-lived eagle species tend to have unusual behavior (Meyburg et al. 2006, 2007).

Finally, this study shows that the combination of a simple metric (i.e., 95% kernel density contour) and a standard statistical technique (i.e., piecewise regression) are a simple but a powerful tool for assessing how long takes eagles to delineate their home range, which is ultimately important for management and decision-taking in conservation actions.

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## **CAPÍTULO 3. Wildfire response of GPS-tracked Bonelli's eagles in eastern Spain.**

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## Abstract

**Background.** Little is known about the interaction between predators and wildfires, in part because the large home range and scarcity of predators make their study difficult, and their response is strongly species-specific. **Aims.** In this paper, we study, for the first time, the effect of wildfire on the behaviour of Bonelli's eagles (*Aquila fasciata*) simultaneously tracked by GPS/GSM dataloggers in four neighbouring territories. **Methods.** One territory was burnt in a wildfire and the other three were used for comparison. We computed the home-range area by comparing individual spatial and temporal behaviour before, during and after the fire event using kernel density estimators and movement parameters. **Key results.** Our results show an immediate negative effect during the first days of the wildfire for an individual inhabiting the burnt territory – the individual flew directly away from the burning area. However, after a few days, the individual recovered their usual behaviour. The three neighbouring pairs did not show significant differences in behavioural parameters before, during and after the wildfire. **Conclusions and implications.** Our results suggest that occasional wildfires do not affect the distribution and density of Bonelli's eagles in the short or medium-term (two years after fire). This could be the result of adaptation by this species to the frequent and recurrent wildfires in the Mediterranean area.

**Keywords:** conservation, datalogger, kernel density, management, Mediterranean, raptors, telemetry, territory.



## Introduction

The current increase in wildfires across the world is likely to have an impact on animal populations (Pausas and Keeley 2019). For instance, there is evidence of decreasing vertebrate populations due to direct mortality by wildfire (Engstrom 2010), or indirectly by changes to habitat quality (Hovick *et al.* 2017). However, there are also examples of vertebrates that were unaffected by or even benefited from wildfire or in a post-fire environment (Jaffe and Isbell 2009; Nappi and Drapeau 2009; Nappi *et al.* 2010; Hovick *et al.* 2017). Many animals may have behavioural traits for dealing with wildfire (Pausas and Parr 2018).

The interaction between vertebrate herbivores and wildfires is quite well known, such as in savannas (Archibald and Hempson 2016) or tropical forests (Cherry *et al.* 2018). However, the interaction between wildfires and predators is poorly documented and understood. This lack of information may be partly because the response to wildfires is highly species-specific in predators (Geary *et al.* 2020), but also because large predators are not abundant and have large home ranges (Lotka 1925), and this makes their study difficult. Nevertheless, the role of wildfire in influencing predator behaviour is of special interest as changes in their population may have cascading effects on trophic networks (Ripple and Beschta 2004; Beschta *et al.* 2018) and, thus, they are crucial in the functioning of ecosystems. Raptors are an example of iconic predators with high conservation value (Donázar *et al.* 2016).

Several studies have focused on the influence of wildfires on the behaviour and conservation of raptors. For example, there is observational evidence of raptors hovering above wildfires and catching animals fleeing the wildfire front or feeding on animals killed by fire (Woinarski and Recher 1997; Smith and Lyon 2000; Bonta *et al.* 2017; Hovick *et al.* 2017). However, flames and smoke can also threaten them by killing individuals, damaging their health, or even destroying their nests. Wildfires also radically change the landscape and vegetation structure and so raptors, even if not directly affected by a wildfire, may be forced to move to



neighbouring landscape areas (Kochert *et al.* 1999). The few published studies on how wildfire affects raptors show both negative (Kochert *et al.* 1999; Blakey *et al.* 2020) and positive effects (Woinarski and Recher 1997; Smith and Lyon 2000; Bonta *et al.* 2017; Hovick *et al.* 2017). The consequences are likely to vary depending on the habitat preferences of the species (e.g. forest and non-forest raptors) although a detailed analysis remains to be done.

We aim to understand the effect of a wildfire on the spatial and temporal behaviour of Bonelli's eagle (*Aquila fasciata*) in a Mediterranean landscape. GPS (global positioning system) telemetry enables us to overcome the difficulties of working with fauna with large home ranges (McGregor *et al.* 2016; Nimmo *et al.* 2019). Here, we leverage information on a wildfire that occurred in the summer of 2016 and affected most of the core of the home range of an eagle (including the cliffs where its nest was located) that was being tracked by GPS telemetry. This provided a unique opportunity to compare the eagle's movements before, during and after the wildfire, and make a comparison with neighbouring eagles simultaneously tracked by GPS telemetry that were unaffected by the wildfire. Finding no differences between preand post-fire home range and movement behaviour would suggest that the spatial ecology of the eagle was unaffected by the fire. In contrast, eagles may be forced to move away to an unburnt area, or expand their home range if the quality of the habitat is reduced by wildfire.

## Materials and Methods

### Species

Bonelli's eagle is a raptor classified as 'near threatened' (NT) in Europe (BirdLife International 2015) and 'vulnerable' (VU) in Spain (SEO/BirdLife 2021). Its habitat includes forest areas, scrub and open areas where there are rabbits, hares, pigeons, corvids and partridges (López-López *et al.* 2006; Martínez-Miranzo *et al.* 2016). According to the latest national survey, conducted in 2018, it is

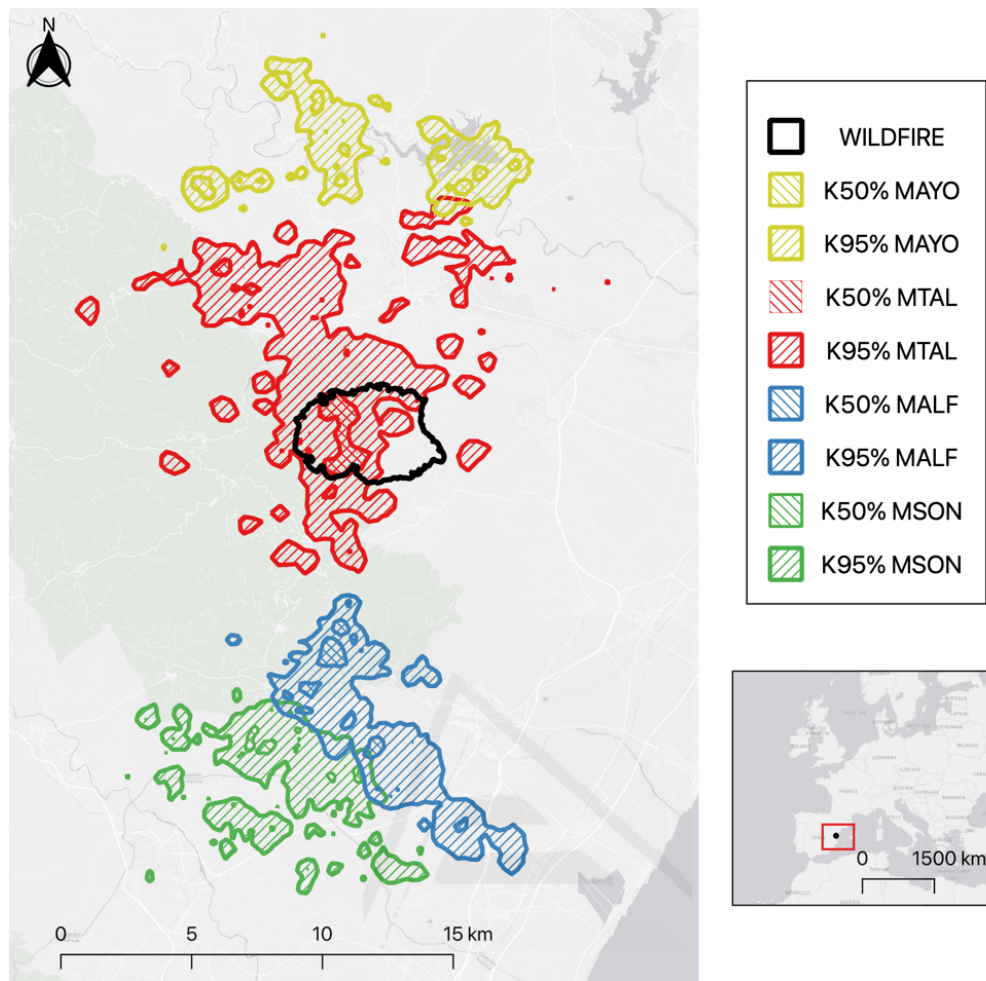
estimated that there are between 711 and 745 pairs in Spain, nesting mainly in cliffs and trees (Del Moral and Molina 2018).

## Study area

This study was carried out in the south of the province of Castellón (eastern Spain; Figure 1). The breeding territories of the eagles were in the Sierra de Espadán Nature Park (from 40°09'N to 39°36'N) and its surroundings. The area covers approximately 400 km<sup>2</sup> and varies from 100 to 1106 m above sea level. The climate is Mediterranean with an average annual temperature that varies between 17°C in the coastal areas and 8°C in the inland mountains. The landscape includes various types of vegetation, mainly patches of pine forest (*Pinus halepensis*, *P. pinaster*), evergreen oak forests (*Quercus rotundifolia*, *Q. suber*) and Mediterranean scrub (*Rosmarinus officinalis*, *Quercus coccifera*, *Cistus* sp.).

The area also includes unirrigated and irrigated farmlands, the former located in the interior and the latter in coastal areas. The study region is highly populated as it is located approximately 50 km from two metropolitan areas of more than 1.5 million inhabitants in total (Castellón and Valencia; National Institute of Statistics, [www.ine.es](http://www.ine.es)).

In summer 2016, a wildfire (the Artana wildfire) affected 1556 ha of the study area and was active between 25 July and 1 August 2016. The municipalities of Alcudia de Veo, Artana, Onda and Tales were affected. The fire advanced during the first 3 days (25–27 July) (see Supplementary Figure S1). This wildfire affected 100% of the core territory (including the nesting site) of one pair of eagles that was being GPS-tracked (named Carbo and Carla, in the municipality of Tales) (Figure 1).



**Figure 1** Locations of the four territories of the males from each pair of the Bonelli's eagle in the study area (Male AYODAR, Male TALES, Male ALFONDEGUILLA and Male SONEJA; see Supplementary Table S1). Territories are indicated as the 50 and 95% kernel distribution obtained from GPS locations. The wildfire (black line) affected the core of the territory of one pair of Bonelli's eagles (MTAL, named Carbo; in red).

## Tracking

A total of four territorial pairs of Bonelli's eagle were fitted with 48-g solar-powered GPS/GSM (Global System for Mobile communication) dataloggers (e-obs GmbH, München, Germany). The territories are located in the municipalities of Alfondeguilla, Tales, Soneja and Ayódar (Figure 1; see Supplementary Table S1). In each of these territories, male and female pairs were captured at the same time (between 2015 and 2016; Supplementary Table S1). The weight of the dataloggers was 1.66–2.86% (average 2.25%, s.d.o. 38%) of the body mass of the eagle, i.e. below

the 3% threshold established to avoid negative effects on animal behaviour (Kenward 2001). The duty cycle of the dataloggers was programmed to record a GPS location at 5-min intervals. Tags were affixed in a backpack configuration using a Teflon tubular harness designed to ensure that it fell off at the end of the tag's life. GPS data were retrieved, stored and managed through the Movebank online repository (<http://www.movebank.org/>).

The female in Tales (named Carla or F\_TAL; Supplementary Table S1), which was one of the pair in whose home range the wildfire occurred, lost her datalogger on 20 April 2016 and thus was not tagged during the wildfire (July–August 2016). She was recaptured and tagged again on 12 December 2016.

### **Ethics statement**

Handling activities were authorised and conducted with permission issued by regional authorities (Conselleria de Agricultura, Medio Ambiente, Cambio climático y Desarrollo Rural, Generalitat Valenciana) and all efforts were made to minimise handling time to avoid any suffering for the eagles.

### **Data analysis**

The Artana wildfire directly affected the territory in Tales where a male individual (Carbo, M\_TAL) was tagged. We first studied the movements of this eagle during the wildfire by analysing distances in relation to the fire ignition point (UTM (Universal Transverse Mercator) coordinates 30S 735229, 30S 4421213). To do so, we considered GPS locations in accordance with the available information on the progression of the wildfire provided by the Valencia Fire Service (Dirección General de Prevención de Incendios Forestales, Generalitat Valenciana). We also analysed the eagle's residence time as the number of hours within the wildfire perimeter in each entry for the periods between 1 June and 31 August (i.e. including the days of the fire). This was done using the R package '*recurse*' (Bracis *et al.* 2018; R Core Team 2018). A non-parametric Kruskal–Wallis analysis was made to identify if there were differences in the travelled distance during the wildfire or the

residence time before and after the wildfire. We animated the movements of M\_TAL during the wildfire with the R package ‘*moveVis*’ (Schwalb-Willmann *et al.* 2020).

We then used the overall territories of the four Bonelli’s eagles – which included seven individuals (Supplementary Table S1) – to compute home-range indicators using kernel density estimation methods (KDE) (Worton 1989) for three short-term periods: before (1 June–24 July), during (25 July–1 August), and after (2 August–31 August) the wildfire.

Specifically, we computed daily 50 and 95% kernels (K50 and K95% respectively) using the R package ‘Reproducible Home-Range’ (*rhr*) (Signer and Balkenhol 2015). We also computed the total daily distance travelled (TDD) and the average daily distance travelled between consecutive points (or step length mean, SLM), using the R package ‘Animal Movement Tools’ (*amt*) (Signer *et al.* 2019). These indicators were computed using 10 947, 1735 and 6199 GPS locations, on average, before, during, and after the fire respectively (Supplementary Table S2). Pairwise comparisons between periods for each variable and for each individual were performed with a non-parametric Kruskal–Wallis analysis and a post-hoc Wilcoxon test by pair samples (Supplementary Table S3 for statistical details). Territorial maps for the seven individuals were made to visualise the kernel density estimators’ results before–during–after the wildfire.

For M\_TAL, we also computed the four home-range indicators (K50, K95%, TDD and SLM) for the same dates as the fire year (before, during and after) but in the next and the second year after the wildfire (i.e. in 2017 and 2018). A non-parametric Kruskal–Wallis analysis was carried out to identify any differences in home-range indicators for the same dates as the wildfire in the following years.

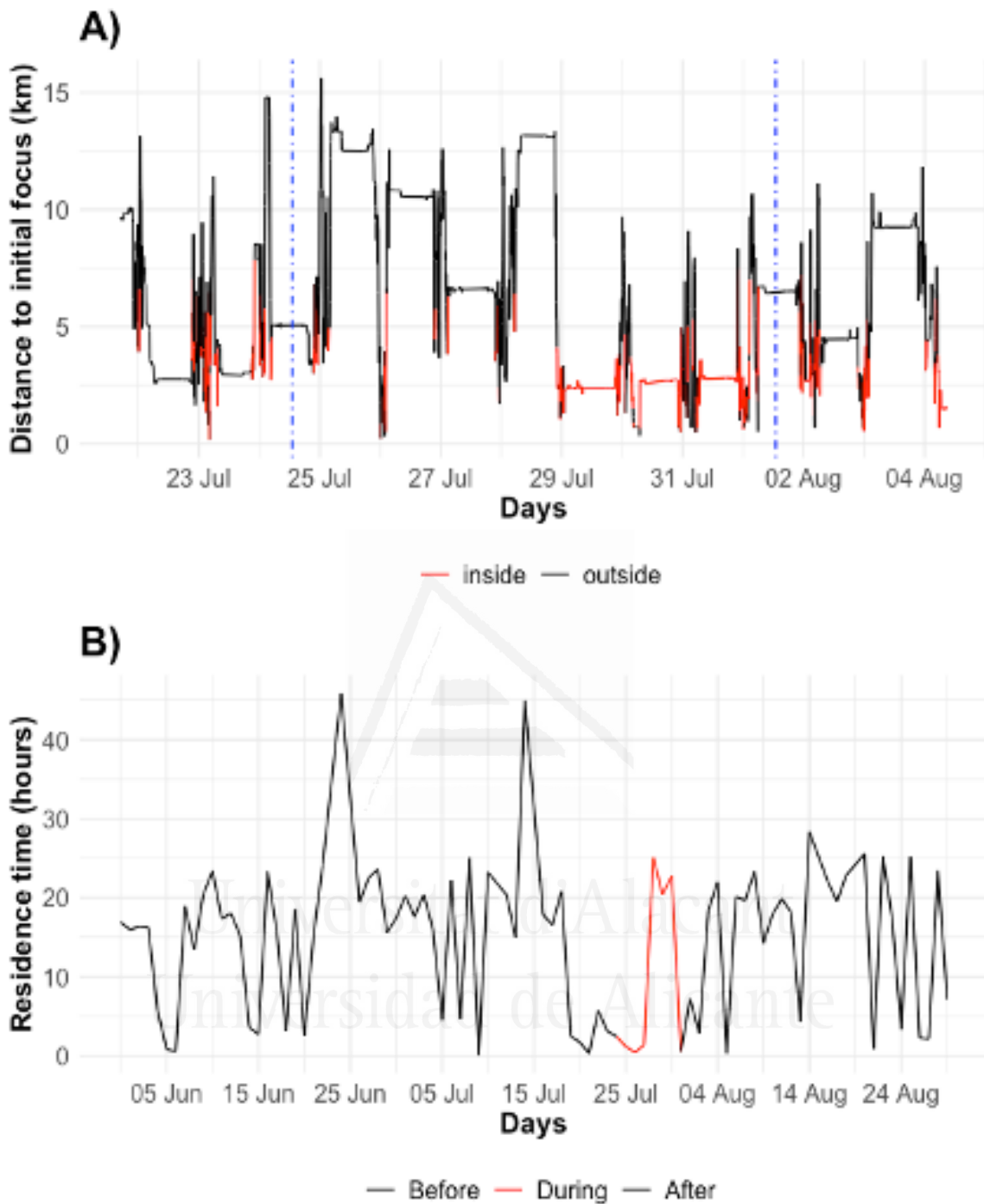
Finally, we computed the same home-range indicators (K50, K95%, TDD and SLM) for the territories of the same four Bonelli’s eagles (10 individuals; long-term analysis in Supplementary Table S1) for periods that expand larger temporal windows as follows: (i) from the tagging day until the day before the wildfire (24

July); (ii) from the day after the wildfire (2 August) until the end of 2016; (iii) throughout 2017 (first year after the wildfire); and (iv) throughout 2018 (second year after the wildfire). During these longer periods, some tagged individuals died, some GPS tags stopped working, and some individuals were replaced – and so the 10 individuals were considered in total (Supplementary Table S2). There is evidence that the replacement individuals assumed the same territorial behaviour as the previous ones (Perona *et al.* 2019; López-López *et al.* 2021). Thereby, the final number of GPS locations used in the analyses were on average 35 193, 18 652, 50 556 and 37 253 for each temporal window, respectively (see Supplementary Table S2 for details). Pairwise comparisons between periods for each variable and for each individual were performed with a non-parametric Kruskal–Wallis analysis and a post-hoc Wilcoxon test by pair samples (see Supplementary Table S4 for statistical details). For all statistical analyses, a significance level of  $P < 0.05$  was set.

## Results

### Movement of the individual directly affected by wildfire

During the first days of the wildfire, the male in the Tales territory (M\_TAL) moved away from the flames (Figure 2A). From the fifth day, however, this individual returned to the fire and spent most of the time within the fire perimeter, even when the fire was still burning (Figure 2a). That is, the distance of the individual to the ignition point was significantly higher during the first fire days (25–28 July;  $8.35 \pm 3.44$  km, range: 0239.24–15.63 km) than after (29 July–1 August;  $3.47 \pm 3.25$  km, range: 0346.35– 13.33 km;  $P < 0.001$ , Kruskal–Wallis test). The proportion of GPS locations (i.e. the proportion of time) within the wildfire perimeter was much lower during the first period (6.02%,  $n = 748$ ) than after (60.37%,  $n = 752$ ). The residence time of the male within the fire perimeter was similar before ( $15.24 \pm 9.99$  h per entry) and after fire ( $14.80 \pm 9.42$  h per entry;  $P = 0.059$ , Kruskal–Wallis test; Figure 2B).



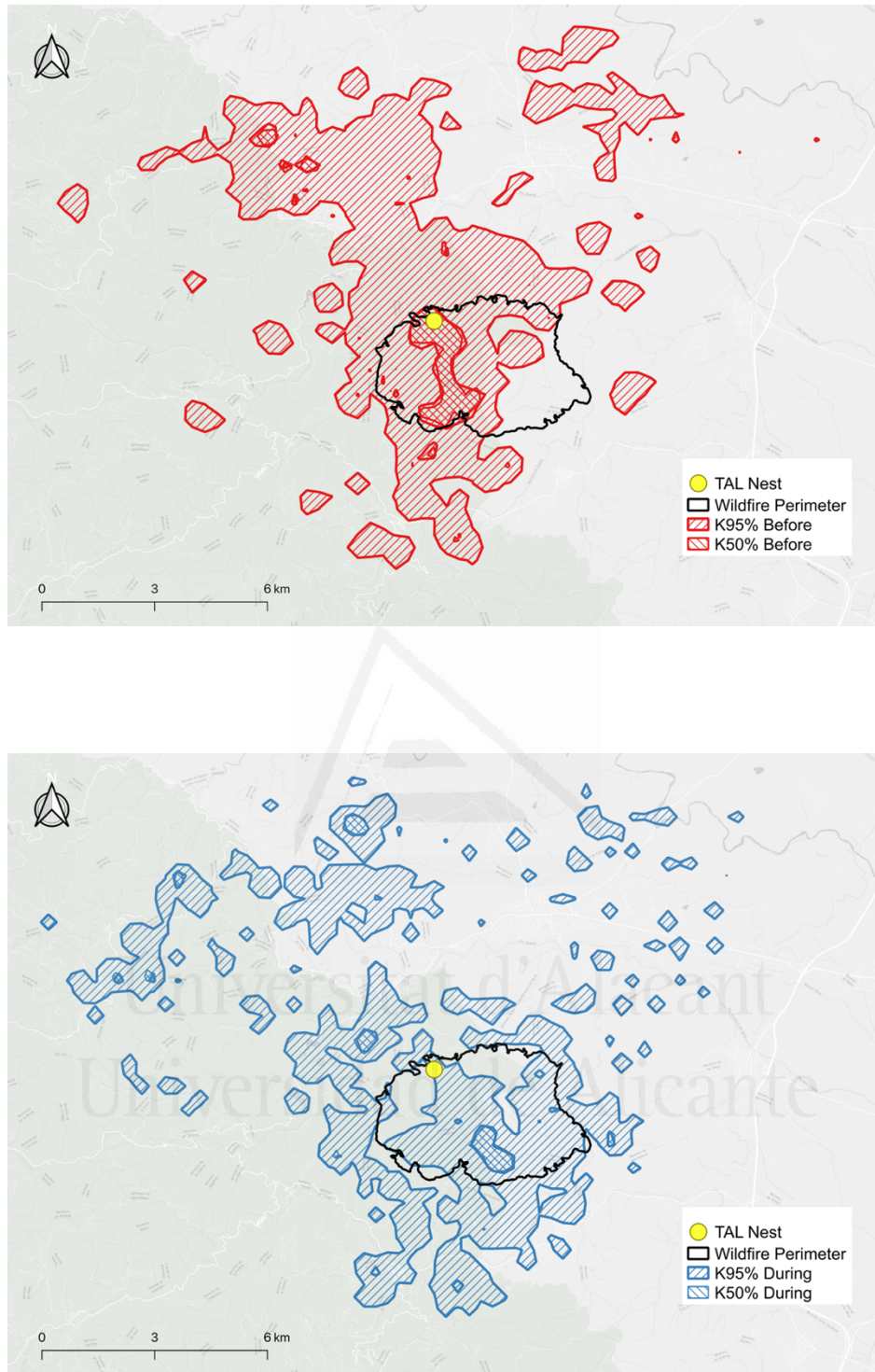
**Figure 2** Behaviour of the male Bonelli's eagle directly affected by the wildfire (M\_TAL) before, during and after the fire event. (A) Distance (km) of the individual from the fire ignition point between 22 July and 5 August (in red when it was within the fire perimeter; the vertical blue lines indicate the beginning and end of the wildfire). (B) Residence time (h) within the fire perimeter between 1 June and 31 August (red line shows the time when the wildfire took place).

Looking at the detailed movements of this male, we observed that this individual moved 6km away from the ignition point in the first 2 h of the fire, following the wind direction (NW), but remained within its home range. The wildfire reached 85% of its final extent that night and affected the nest where two chicks had fledged a couple of months previously. The next day, there were still some active fire fronts and considerable firefighter activity in the study area (including the continuous movement of firefighting planes). The individual remained outside the burnt area and at the limits of its territory. It then made a change in its direction from west to east at 11 am, and visited the initial point of the wildfire, where the flames were already extinguished. At 1 pm, this individual crossed most of the burnt area, heading northwards, and remained outside the rest of the day. A similar pattern was observed during the following days, when it never left its territory and flew over the edges of the wildfire even when there was still some fire activity. It flew over areas that were burning slowly (without the wind of the first days). On the last day of the wildfire, the individual remained most of the day within the burnt area in the southern part of its territory where the wildfire originated, and for the first time since the wildfire, it spent the night within the burnt area (see an animation of these movements in Figshare Repository 10.6084/m9.figshare.19209918).

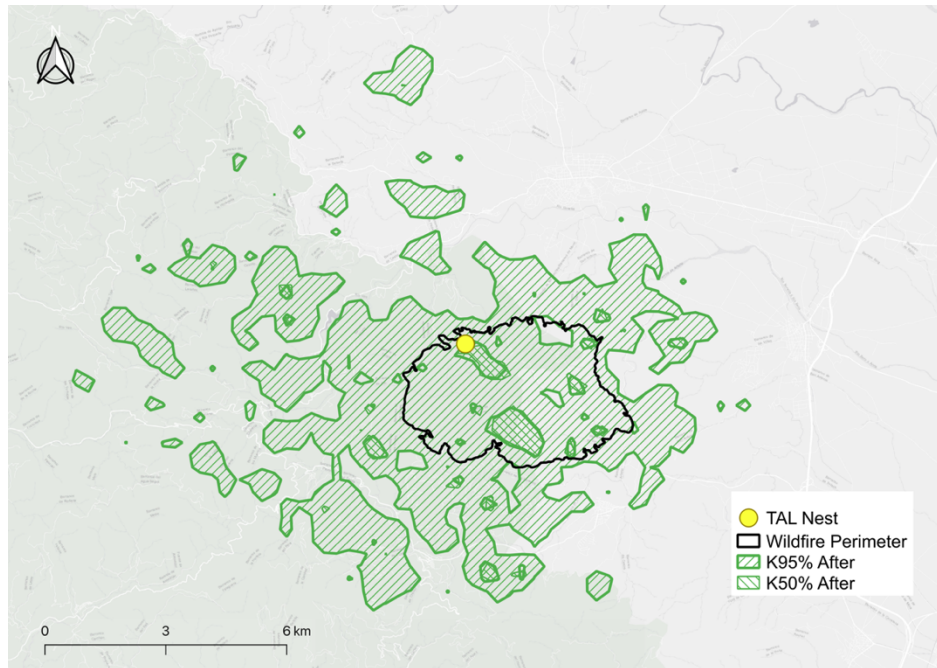
### **Short-term differences in home-range**

The 95% kernel of M\_TAL increased during the wildfire, but it quickly decreased to pre-fire levels straight after (Figure 3, Supplementary Figure S2, Supplementary Table S3 for statistical details). A similar but not significant pattern was observed for the 50% kernel (i.e. the core area) and the distances travelled (TDD, SLM, Figure 3). The pair in Alfondiguilla (named M\_ALF and F\_ALF) that were ~4.5 km from the fire also showed some increase in their 95 and 50% kernels during the wildfire – and quick recovery (Supplementary Figure S2, Supplementary Table S3 for statistical details; Supplementary Figs S3, S4 for map territories).





**Figure 3** Home range according to the spatial estimator 95 and 50% kernels of the male Bonelli's eagle directly affected by the wildfire (M\_TAL). The fire perimeter (black polygon) and nest (yellow dot) are shown: (A) before the wildfire (red; 1 June–24 July); (B) during the wildfire (blue; 25 July–1 August).



**Figure 3** Home range according to the spatial estimator 95 and 50% kernels of the male Bonelli's eagle directly affected by the wildfire (M\_TAL). The fire perimeter (black polygon) and nest (yellow dot) are shown: (C) after the wildfire (green; 2 August–31 August).

The other two pairs (located in Soneja and in Ayódar municipalities – 6.8 and 8.6 km away from the wildfire) were also weakly affected by the wildfire according to their home range as estimated with 95 and 50% kernels (Supplementary Figure S2, Supplementary Table S3 for statistical details; Supplementary Figs S5–S8 for map territories).

### Long-term differences in home-range

The pair that was affected by the wildfire (i.e. M\_TAL and F\_TAL) hatched two chicks in 2016. In the year after the fire (2017), they did not hatch any chicks, and they hatched one in 2018. In 2017, for the same dates, there were significant differences in the 50% kernels ( $P = 0.031$ ; Kruskal–Wallis test) of the male before ( $7.13 \pm 5.29 \text{ km}^2$ ), during ( $4.90 \pm 3.15 \text{ km}^2$ ) and after ( $10.18 \pm 6.89 \text{ km}^2$ ) the fire. This is the opposite pattern to 2016 (the year when the fire occurred). There were no differences in the remaining variables. In the following year, 2018, and for the same

dates, there were no significant differences in any of the four variables considered (all  $P > 0.05$ ; Kruskal–Wallis test).

If we compare the four long-term periods (i: from tagging date to the wildfire; ii: from the wildfire to the end of 2016; iii: for 2017; and iv: for 2018) for each of the eight individuals (four pairs), there were no differences in any of the variables considered in this study (95% kernel, 50% kernel, TDD, and SLM) for any individual (see Supplementary Table S4, Supplementary Figs S9–S12).

## Discussion

We show, for the first time, the effect of fire on the spatial and temporal behaviour of a Bonelli's eagle, an endangered European raptor. Because these eagles had been previously tagged with GPS telemetry, we were able to analyse in detail the response of a Bonelli's eagle to wildfires. Previous studies on the goshawk (*Accipiter gentilis*; Blakey *et al.* 2020) and on the golden eagle (*Aquila chrysaetos*; Kochert *et al.* 1999) concluded that both species were negatively affected by fire owing to forest habitat destruction in the first case and post-fire reduction of its main prey (rabbits) in the second case. Urios (1986) analysed the distribution of Bonelli's and golden eagle territories, including those that had been burnt in recent years, and concluded that wildfires did not affect the distribution of Bonelli's eagle in Valencia (Spain). In contrast, wildfires were a significant positive factor for the golden eagle, probably owing to the increased availability of open habitats that favour prey and accessibility for hunting. In contrast, Kochert *et al.* (1999) showed that wildfires decreased the breeding performance of golden eagles in the first 4–6 years after large wildfires (increasing afterward).

Also, Tapia *et al.* (2017) showed how land cover change (e.g. through high-intensity, low-frequency fires) can negatively affect forest species owing to possible loss of forest canopy. However, species that are not strictly forest specialists, such as the common buzzard (*Buteo buteo*) may benefit from open habitats (e.g. scrublands) for hunting.

Despite a wildfire affecting most of the eagle's core area (according to the 50% kernel density contour), its activity was hardly affected and the individual moved away from the fire but did not leave its home range (95% kernel). The reason why it did not leave its territory may be related to interactions with neighbours, as this species is highly territorial (Urios 1986). The consistency in the spatial behavior of this individual the two years following the fire suggest that changes observed during 2016 were probably due to the wildfire event.

Fortunately, there were three additional neighbouring Bonelli's eagle pairs that were also simultaneously GPS tracked. The home-range areas of these three pairs were not directly burnt by the wildfire. Some showed changes in their activity during the fire dates but quickly recovered after the wildfire (Supplementary Figure S2). We consider that these slight changes in their activity could be a direct response to the smoke, or more likely, to the high level of firefighting activity in the area (which included off-road vehicles and firefighting planes).

Our results suggest that Bonelli's eagles were unaffected by wildfires in the short and medium term. Bonelli's eagles, like other birds, can move away when a fire is burning hot. However, their spatial and temporal behavioural response after the catastrophic event did not differ from that observed before. Our results did not show any change in their behaviour during the 2 years after the wildfire. In fact, the pair whose territory was directly affected by the fire reproduced successfully in the second year after the wildfire on the same cliffs (some of which were completely burnt). Note that long-lived raptors do not breed every year (Steenhof and Newton 2007). The resilience of this species to wildfires was already suggested after overlaying regional distribution maps of this species in eastern Spain on fire frequency maps (Urios 1986). Our results suggest that the main prey (rabbits and pigeons) were unaffected by the wildfire. This could be explained by the ability of many small mammals to survive fire by sheltering in burrows (Geluso and Bragg 1986). Burrowing behaviour could be an adaptive response in animals in fire-prone ecosystems (Long 2009; Pausas and Parr 2018). In addition, fires increase open spaces and while this favours rabbits (Moreno and Villafuerte 1995), Bonelli's

eagles may also benefit from the increased visibility of their prey after a fire. In general, post-fire conditions increase the attractiveness of burnt areas to predators (Leahy *et al.* 2016; McGregor *et al.* 2016), including other raptors (Barnard 1987; Hovick *et al.* 2017) and colonisation may occur from nearby areas, as they take advantage of these newly available open areas.

Negative consequences of wildfires on raptors have been documented, for instance, in forest species (Blakey *et al.* 2020). However, in fire-prone ecosystems such as those of the study area, located in the European Mediterranean region, it is likely that many species, both flora and fauna, could be able to deal with some fire activity (Pausas and Keeley 2019). Animal adaptation to fire is not easy to detect, but there is increasing recognition of the importance of understanding behavioural traits to assess animals' response to wildfires (Pausas and Parr 2018; Nimmo *et al.* 2019; Álvarez-Ruiz *et al.* 2021). Further, this knowledge is urgently needed for a wide range of species as the Earth is warming and fire regimes are quickly changing (Pausas and Keeley 2021). Our study case is based on a fairly small fire (~1500 ha), yet it has allowed us to improve our knowledge on the response of a European endangered species to a global change driver.

Finally, it is worth noting the importance of this serendipitous event, as we were able to analyse the behavioural response of several individuals of the same species distributed across neighbouring territories thanks to a fire occurring where eagles were already being tracked simultaneously by GPS-telemetry.

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Universitat d'Alacant  
Universidad de Alicante

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## **CAPÍTULO 4. A new view of territoriality. Design of protected areas with its application.**

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**Manuscrito en revisión:** Morollón, S., López-López, P. and Urios, V. (*in review*).

A new view of territoriality. Design of protected areas with its application.

*Ornithological Applications.*





## Abstract

The knowledge about territoriality and space use by predators is a topic of great interest in the study of animal behavior and conservation biology. Examining the plasticity of territory limits, the topography, and how territories can be modified depending on their owners is important to deepen the territorial species' behavior. We analyzed the variations and tested the similarity of the home range of individuals from the same territory using the data provided by 51 Bonelli's eagles from 22 different territories, tagged with GPS/GSM dataloggers in eastern Spain. We analyzed the percentage of overlap of the annual home range considering the 95% kernel density estimator between individuals of the same territory. Also, we analyzed the variation in the home range size according to three different kernel levels (95%, 75%, and 50%) and the annual eccentricity of each home range as a complementary metric to study the topography of territories across years. We also analyzed the changes in territory size and topography after the replacement of territory owners either by a single individual or by the entire pair. Our results show that territories, regardless of the occupying members, have the same topography and extension and that their limits hardly vary across time. Therefore, the identification and conservation of territories of large eagles regardless of their owners are key to ensuring species recovery in the long term, which is particularly important for endangered species. Finally, our study highlights satellite telemetry's importance in further investigating behavioral ecology and its conservation implications in large eagles.

**Keywords:** animal behavior, *Aquila fasciata*, Bonelli's eagle, datalogger, GPS technology, home-range, satellite telemetry.





## Introduction

The study of spacing patterns and territoriality is essential for many aspects of our understanding of animal populations. There are several criteria for defining territoriality in animals. One of them could be from a behavioral point of view, there are different forms of territoriality, such as area-defended territoriality (Brown 1975; Wilson 1975; Kaufmann 1983; Maher and Lott 1995) or site-specific dominance territoriality (Emlen 1957; Wittenberger 1981). And also it might be defined from an ecological point of view (Maher and Lott 1995). In addition, territories may vary due to population density, food quantity and quality, habitat characteristics, and the individuals inhabiting them (Maher and Lott 2000).

The description and use of the territories by different species of vertebrates have been described since the beginning of zoology and animal behavior studies. Most of these studies have been based on large mammals (e.g. Lorimer 2010; Kalan et al. 2016), large predators (e.g. Cruz et al. 2021), and large raptors (e.g. Newton 1979; Ferrer and Bison 2003; Blas and Hiraldo 2010; Bosch et al. 2010; Hernández-Matías et al. 2010). We find studies that analyze the behavior and use of space in reproductive cycles (e.g. López-López et al. 2016a), feeding (e.g. Barton and Houston 1994; Costantini et al. 2005), territorial occupation (e.g. Martinez et al. 2008) and habitat selection (e.g. Tanferna et al. 2013; Barrientos and Arroyo 2014). However, the determination that territories exist as a singular element by themselves has not been studied to date (Fryxell, and Lundberg 1997; Adams 2001; López-Sepulcre and Kokko 2005).

The Bonelli's eagle (*Aquila fasciata*) is a strongly territorial raptor that defends its territory in pairs, exhibiting typical behavior in which males and females fly together for cooperative hunting. This species shows a large distribution across Europe, North Africa, and southern Asia. In Europe, it occupies Mediterranean habitats with Mediterranean evergreen forests and an abrupt orography. The species is classified as "Near Threatened" (NT) in Europe (BirdLife International 2015) and "Vulnerable" (VU) in Spain (SEO/Bird-Life 2021).

Currently, when considering the limits and zoning of protection areas for specific species, as in the case of the EU Special Protection Areas (SPAs; Council Directive 79/409/EEC of 2 April 1979 on the conservation of wild birds), the location of nests is taken into account and the proposed limits usually coincide with geographical features or areas that are easy for the administrations to delimit. The proposal presented here would imply a new criterion for the delimitation of these limits, as it would include the limits of occupied territories and even unoccupied territories, perhaps allowing a better recovery of the species.

The objective of the present work is to test whether the existence of stable and defined territories is independent of their owners. To this end, we use telemetry (GPS/GSM) data information to examine the plasticity of territory limits, the topography, and how territories can be modified depending on their owners. Here, to this end, we evaluate the space use of different Bonelli's eagles (*Aquila fasciata*) individuals within the same territory on eagles' ranging behavior across years. If the territory is fixed independently of its occupants, no differences in annual home range size and the territory eccentricity (distance between the arithmetic center of territory to the nest location) would be expected between individuals that occupy each territory during consecutive years (i.e., the null hypothesis). In contrast, each individual of one territory may show different space use patterns and thus annual home range size and territory eccentricity should be different between individuals that inhabit the same territory across time (i.e., the alternative hypothesis).

## Materials and Methods

### Study area

The study area is located in eastern Spain including Albacete, Alicante, Castellón, Cuenca, and Valencia provinces. The area covers approximately 10 000 km<sup>2</sup> with an average altitude ranging between sea level and 1500 m a.s.l. The climate is Mediterranean with an average annual temperature that varies between

8°C in the interior mountains and 17°C in the coastal areas. The dominant landscape is composed of Mediterranean scrublands, oak forests (*Quercus faginea*, *Quercus suber*), and Mediterranean evergreen forests (*Quercus ilex*, *Pinus halepensis*, and *Pinus nigra*).

## Tracking

Adult and subadult Bonelli's eagles were trapped in their breeding territories and tracked between 2015 and 2021. In some cases, individuals were trapped and tagged in the same territory after the death or disappearance of one or both occupants (Table S1, see Supplementary Material). All individuals were tagged with GPS/GSM solar energy dataloggers manufactured by e-obs GmbH (Munich, Germany) and Ornitela (Vilnius, Lithuania) using a backpack configuration employing a Teflon tubular harness designed to ensure that the harness fell off at the end of the tag's life. The weight of the transmitters was 48 and 50 g, respectively, and represented 1.66 to 2.86% (mean = 2.25%, SD = 0.38%) of the body mass of eagles, below the 3% threshold established to avoid negative effects on behavior (Kenward 2001; García et al. 2021). The duty cycle of the transmitters was programmed to record a GPS location at five-minute intervals (López-López et al. 2021), from 1 h before sunrise to 1 h after sunset, year-round during the study period (2015 – 2021). Transmitters' data was retrieved, stored, and managed through the Movebank online repository (<http://www.movebank.org/>).

## Ethics statement

Trapping and marking activities were authorized and conducted under permissions issued by regional authorities (Conselleria de Agricultura, Medio Ambiente, Cambio climático y Desarrollo Rural, Generalitat Valenciana, Spain) and all efforts were made to minimize handling time to avoid any suffering to eagles.

## Home-range and space use analysis

We used kernel density methods (KDE) (Worton 1989) to calculate home range size and evaluate space use. We computed different levels of kernel isopleths as follows to allow comparison with similar studies: the 95% kernel isopleth (K95%) was considered as the total area of the home range (Samuel et al. 1985); the 75% kernel isopleth (K75%) was considered as the intermediate area of active use, which includes the feeding and resting areas; and the 50% kernel isopleth (K50%) is the core area of the home range, where the nest is usually found (Kie et al. 2010). The isopleths are the curves that connect the points where the function has the same constant value. We obtained these kernel levels from the next day after tagging to the end day of data transmission (e.g. animal's death, end of transmission) using the "reproducible home range" (*rhr*) R package for statistical computing (Signer and Balkenhol 2015; R Core Team 2020). Secondly, we computed the eccentricity of each territory as the distance from the arithmetic center of all the annual K95% locations (i.e., the centroid of the polygon) of each individual to the nest location within each territory. The *rgeos* and *raster* R packages were used to calculate the eccentricity (Bivand and Rundel 2020; Hijmans 2020).

## Data analysis

We analyzed the annual territorial overlap between the different individuals that occupied the same territory across the years. To this end, we calculated the percentage of annual overlap between the total home ranges sizes (K95%) of individuals from the same territory using the *raster* R package (Hijmans 2020). Furthermore, we use a Generalized Linear Mixed Model (GLMM; following the suggestions described in Zuur et al. 2009) to analyze the variation of annual home range size and the eccentricity within each territory, considering "Territory" as a random factor. The variation is examined about three fixed factors, "Year", "Sex" and animal "ID". Annual home range sizes according to the three different spatial estimators (K95%, K75%, and K50%) and the annual eccentricity were logarithmically transformed and were used as the response variable. The R package

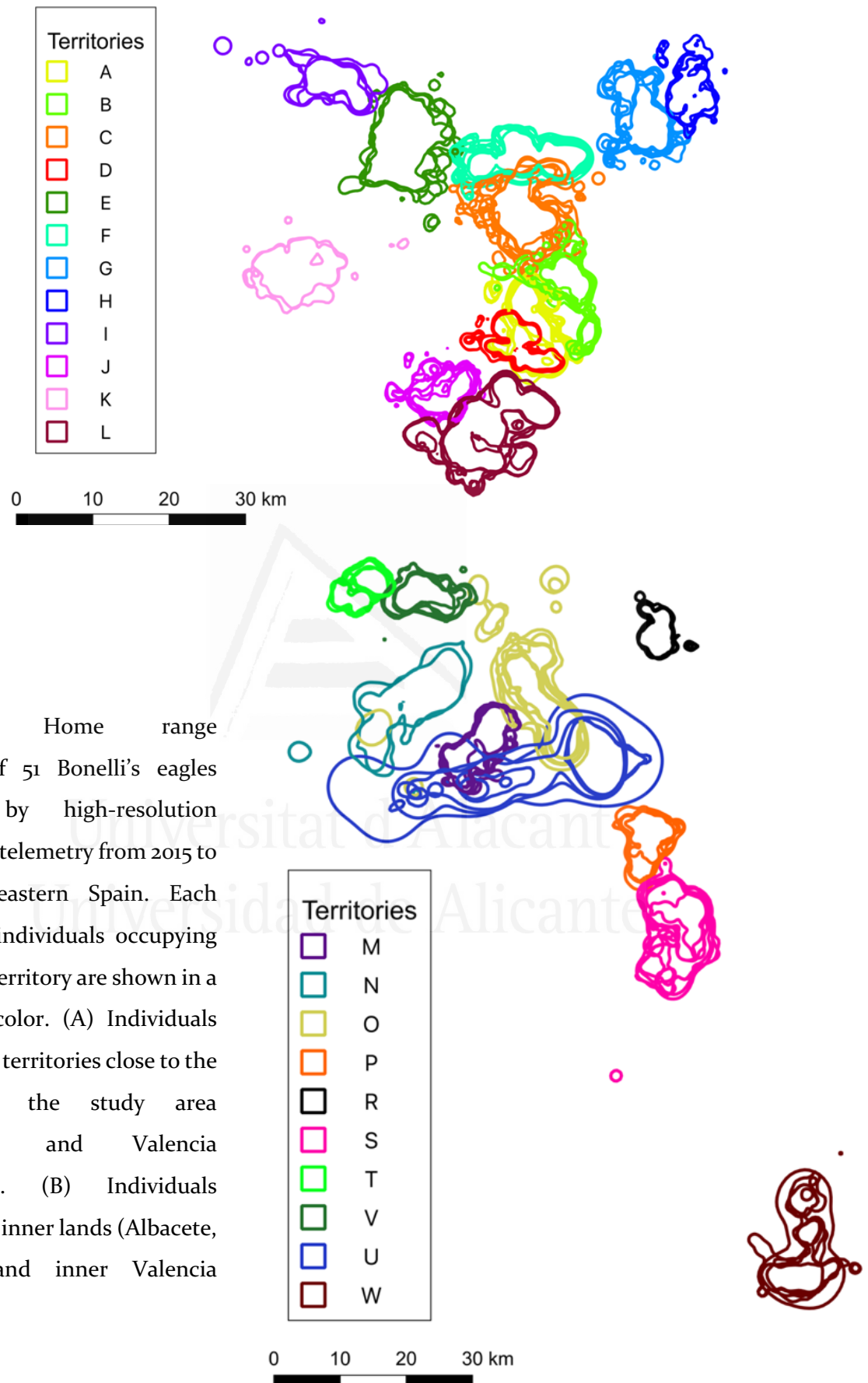
used for the analysis was *lme4* (Bates et al. 2015). We also computed the correlation between the home range area according to the K95% and the eccentricity to check the relationship between both parameters and the morphology of the territories. We further described in detail the turnover events in which a territory owner was replaced by another individual who was subsequently tagged. In these cases, we computed the percentage of overlap between the home ranges of those individuals (previous and new ones).

## Results

Overall, we obtained 4 791 080 GPS locations (mean = 101 098.42; SD = 81 578.23; range = 1016 – 257 640 locations) of the 51 eagles that were tracked in this study. A total of 26 males and 25 females, were trapped in 22 different territories (Figure S1 in Supp. Mat.).

### Annual territorial overlap among individuals of the same territory

On average, the overlap between home range area within territories was  $80.95\% \pm 13.44\%$  (n=1160 overlapping percentages between and within territory occupants during the tracked years; with a range of  $91.03 \pm 4.71\%$  (Territory R, n=30) -  $71.99 \pm 24.08\%$  (Territory U, n=12; Figure 1; Figure S2 and Table S3-S24, in Supp. Mat.). In the GLMM analysis, the variance explained by random factors was 0.55, 0.42, and 0.40 for K95%, K75%, and K50%, respectively. There were no differences in the home range size within each territory between different individuals ("ID", K95%:  $F=1.396$ ,  $p=0.054$ ; K75%:  $F=1.113$ ,  $p=0.294$ ; K50%:  $F=1.095$ ,  $p=0.322$ ) and among years ("YEAR", K95%:  $F=0.990$ ,  $p=0.436$ ; K75%:  $F=1.153$ ,  $p=0.338$ ; K50%:  $F=1.446$ ,  $p=0.204$ ). However, there were differences in the home range size between sexes within territories, being larger males' home range size (K95%:  $85.5 \pm 62.9 \text{ km}^2$ ; K75%:  $30.6 \pm 20.8 \text{ km}^2$ ; K50%:  $11.2 \pm 7.1 \text{ km}^2$ ) than females' home range size (K95%:  $73.70 \pm 43.19 \text{ km}^2$ ; K75%:  $25.5 \pm 15.4 \text{ km}^2$ ; K50%:  $9.2 \pm 5.9 \text{ km}^2$ ) ("SEX"; K95%:  $F=5.458$ ,  $p=0.021$ ; K75%:  $F=13.196$ ,  $p<0.001$ ; K50%:  $F=10.412$ ,  $p=0.002$ ; Table 1; Table S2 in Supp. Mat.).



**Figure 1** Home range overlap of 51 Bonelli's eagles tracked by high-resolution GPS/GSM telemetry from 2015 to 2021 in eastern Spain. Each group of individuals occupying the same territory are shown in a different color. (A) Individuals occupying territories close to the coast of the study area (Castellón and Valencia provinces). (B) Individuals marked in inner lands (Albacete, Cuenca and inner Valencia province).

**Table 1** Generalized Linear Mixed Model (GLMMs) results. Significant values are highlighted in bold.

Value	Variable	F	Df	Df.res	p-value
K95%	<b>Intercept</b>	<b>98.311</b>	<b>1</b>	<b>272.77</b>	<b>&lt;0.001</b>
	ID	1.396	50	233.93	0.054
	<b>SEX</b>	<b>5.458</b>	<b>1</b>	<b>103.00</b>	<b>0.021</b>
	YEAR	0.990	6	103.00	0.436
K75%	<b>Intercept</b>	<b>47.229</b>	<b>1</b>	<b>347.18</b>	<b>&lt;0.001</b>
	ID	1.113	50	241.96	0.294
	<b>SEX</b>	<b>13.196</b>	<b>1</b>	<b>103.00</b>	<b>&lt;0.001</b>
	YEAR	1.153	6	103.00	0.338
K50%	<b>Intercept</b>	<b>22.696</b>	<b>1</b>	<b>283.83</b>	<b>&lt;0.001</b>
	ID	1.095	50	235.45	0.322
	<b>SEX</b>	<b>10.412</b>	<b>1</b>	<b>103.00</b>	<b>0.002</b>
	YEAR	1.446	6	103.00	0.204
Eccentricity	<b>Intercept</b>	<b>6.340</b>	<b>1</b>	<b>1664.69</b>	<b>0.012</b>
	ID	0.813	50	263.44	0.809
	SEX	0.918	1	103.00	0.340
	YEAR	1.482	6	103.00	0.192

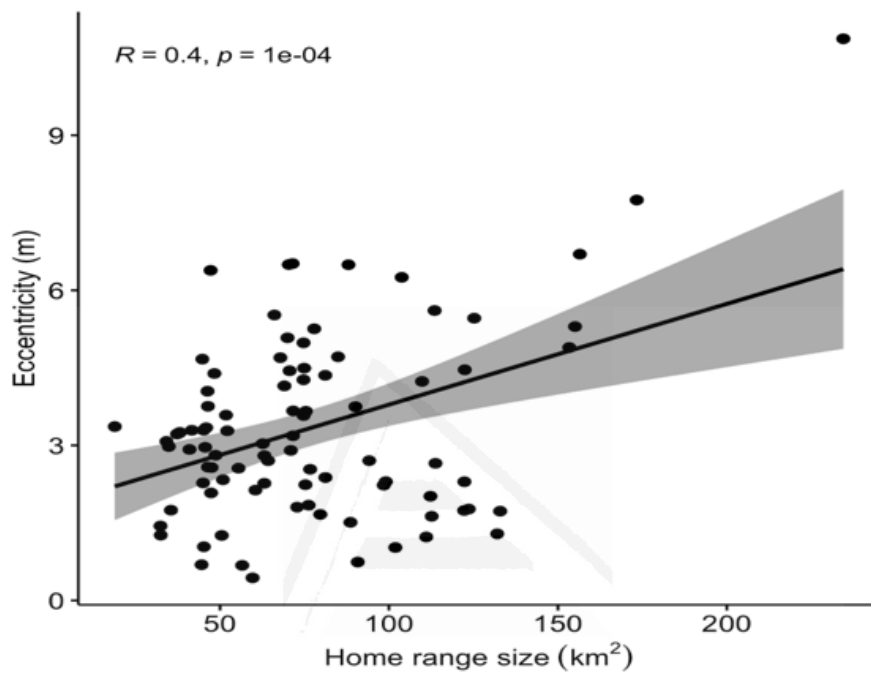
### Annual territorial eccentricity

On average, the annual eccentricity of the territories was  $3530.43 \pm 2021.92$  m (range = 412.88 – 14 242.83 m) (Figure S1 and Table S26 in Supp. Mat.) In the GLMM analysis, the variance explained by random factors was 0.44 for eccentricity. There were no differences in the eccentricity within each territory between different individuals occupying them (“ID”,  $F=0.813$ ,  $p=0.809$ ), among different years (“YEAR”,  $F=1.482$ ,  $p=0.192$ ) and neither between sexes (“SEX”,  $F=0.918$ ,  $p=0.340$ ) (Table 1; Table S2 in Supp. Mat.).



## Correlation between eccentricity and territory size

We found a significant positive correlation between home range size and eccentricity ( $R = 0.4$ ;  $p < 0.001$ ; Figure 2). Therefore, the higher the home range size, the higher the eccentricity.

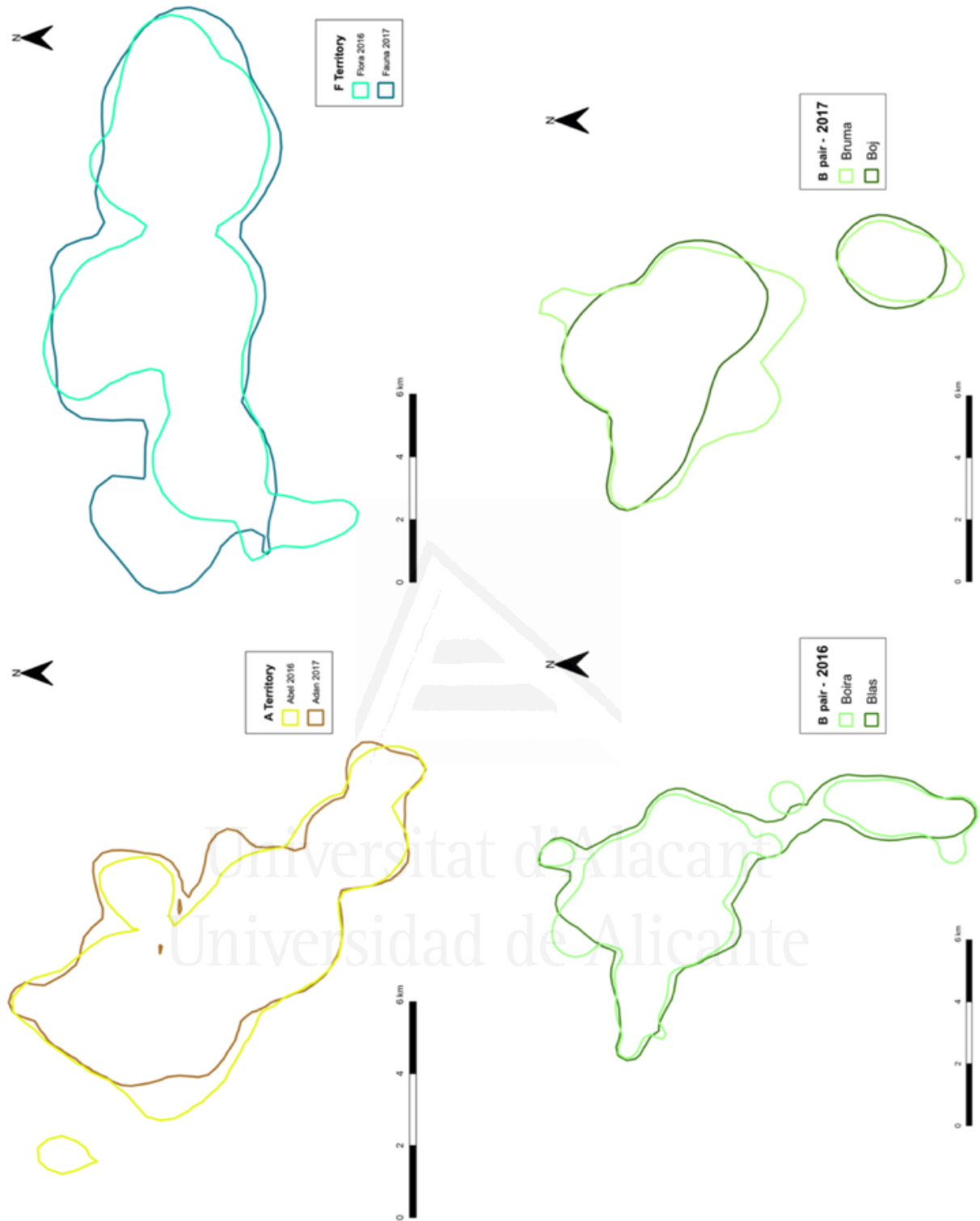


**Figure 2** Correlation between eccentricity and home range size (K95%).

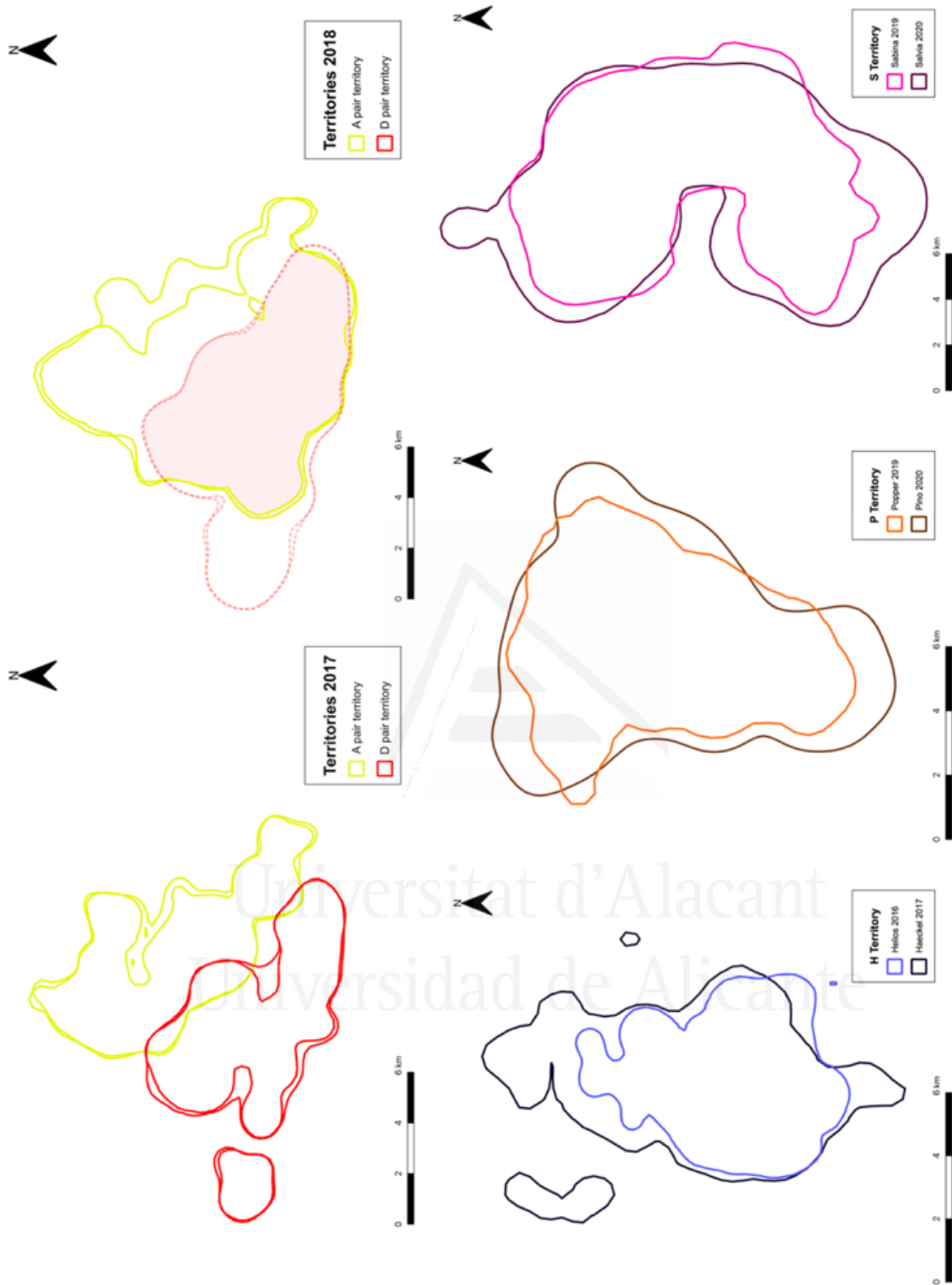
## Turnover events

There were seven territories with replacements in their owners, with eight replacements in total: 1) the A territory had one simple replacement of the male (Abel died in September 2016 by unknown causes and was replaced by Adan, which was tagged in January 2017). The annual overlap percentage of these individuals in consecutive years was Abel 2016 – Adan 2017 = 89.2% (Figure 3A; Table S3 in Supp. Mat.); 2) the B territory had two replacements, one simple replacement of the female (Berta died in July 2015 by a collision with a power line and was replaced by Boira, tagged in November 2015). The overlap percentage of this year was Berta 2015 – Boira 2015 = 66.50%. Also one double turnover of both members of the pair (Boira and Blas drowned in an irrigation pond in June 2016 (López-López et al.

2016b) and were replaced by individuals from the floating population, Boj, and Bruma in 2017, which were tagged at the same time in April 2017). The annual percentage of overlap of home ranges between 2016 and 2017 (the period in which the complete replacement occurred) were: Boira 2016 – Bruma 2017 = 89.7%; Boira 2016 – Boj 2017 = 84.0%; Blas 2016 – Bruma 2017 = 92.2%; and Blas 2016 – Boj 2017 = 84.3% (Figure 3B; Table S4 of Supp. Mat.); 3) the D territory had a double replacement (Dino and Dora were poisoned at the same time in March 2018 (López-López and Urios 2018) and Adan and Aura (neighbors of the A territory) occupied both territories (territories A and D) only two days after the death of the pair Dino-Dora. The annual overlap percentages of the A pair's home ranges compared with the year before the death of the D pair (2017) were between 69.3 – 92.6%. The annual overlap percentages of the new territory emplacement of the A pair's home range on the old D territory (Dino - Dora pair) were between 50.7 – 77.5 (Figure 3C; Table S6 and Table S25 in Supp. Mat.). The 4) the F territory had one simple replacement of the female (Flora died in December 2016 by electrocution at a power line and was replaced by Fauna, tagged in May 2017). The annual overlap percentage between these individuals was Flora 2016 – Fauna 2017 = 93.0% (Figure 3D; Table S8 in Supp. Mat.); 5) the territory H had one simple turnover of the male (Helios died in January 2017 by electrocution at a power line and was replaced by Haeckel, tagged in April 2017). The annual overlap percentage between these males was Helios 2016 – Haeckel 2017 = 95.1% (Figure 3E; Table S10 in Supp. Mat.); 6) the P territory had one simple replacement of the male (Popper died in October 2019 by collision with a power line and was replaced by Pino, tagged in June 2020). The annual overlap percentage between these individuals was Popper 2019 – Pino 2020 = 97.2% (Figure 3F; Table S18 in Supp. Mat.); 7) the S territory had one simple replacement of the female (Sabina died in February 2020 by collision with a fence and was replaced by Salvia, tagged in June 2020). The annual overlap percentage between these females was Sabina 2019 – Salvia 2020 = 99.3% (Figure 3G; Table S20 in Supp. Mat.).



**Figure 3** Comparison of annual home-ranges (K95%) after a turnover event. (A) Turnover between A territorial males. (B) Turnover between B territorial pairs. (C) Turnover between D territory (in red) and A territory (in yellow) in 2017 (top) and in 2018 (bottom). In 2018 the D territory is represented by a dashed red line to remember where was previously.



**Figure 3** (D) Turnover between F territorial females. (E) Turnover between H territorial males. (F) Turnover between P territorial males. (G) Turnover between S territorial females.

## Discussion

Territoriality is one of the most decisive aspects in the ecology and behavior of animals, humans included, with important evolutionary implications. Hence, the study of territoriality in long-lived vertebrates might be a good proxy for this purpose. In this study, we propose a new view of the spatial ecology of large vertebrates by which territories exist independently of the individuals occupying them. To the best of our knowledge, this had not been taken into account in studies of territoriality to date. To this end, we have taken advantage of a large sample size either in terms of the number of locations (4,791,080 GPS locations), the number of territories occupied by different individuals (22 territories), and in terms of study duration (seven years).

### Annual territorial overlap between individuals within the same territory

Our results show that the area and delimitation of territories remain the same over the years regardless of the individuals inhabiting them, with a high mean percentage of overlap between individuals occupying the same territory ( $80.95 \pm 13.44\%$ ). This means that the territory remains constant regardless of whether it is used by one pair, by a new pair, or by a pair formed by a previous and a new individual. Our result of the overlap between different occupants of territory has never been studied before, neither in Bonelli's eagle nor in other vertebrate species. Instead of that, there are previous studies that measured the inter-annual fidelity by each individual or overlap between sexes. The overlap percentage of the occupants of a territory recorded in our study is higher in comparison to these previous studies in Bonelli's eagle of individual overlap percentage recorded by GPS (30.3%,  $n=7$ , Pérez-García et al. 2013; 76.8%,  $n=8$ , Martínez-Miranzo et al. 2016), but lower than the percentage of overlap between sexes recorded by radio-tracking (98.6%,  $n=10$ , Bosch et al. 2010). The overlap percentage is also higher than the percentage of individual inter-annual fidelity overlap described in other raptor species such as the Golden eagle (*Aquila chrysaetos*) (60%,  $n=8$ , radio-tracking, Marzluff et al. 1997; 70% (99% kernel),  $n=17$ , GPS, Watson et al. 2014), and Spanish

imperial eagle (*Aquila adalberti*) (75%, n=8, radio-tracking, Fernández et al. 2009). The higher percentage recorded in this study is probably due to the larger sample size (n=51 individuals) and the higher precision of the raw data (GPS/GSM telemetry versus combined Argos/GPS telemetry or radio-tracking). Therefore, our results show the fidelity and similarity between individuals occupying the same territory and the definition of territorial limits do not change over time.

Interestingly, our results also show that space use could also be oppressed by neighboring territorial pairs. Our overlap analysis shows that the shape of the territory is also maintained in addition to its extension. Moreover, the topography of the territory is not similar between neighboring pairs; whereas some are elongated, others are rounded; others are more irregular, adapting to the physiognomy of the terrain and maintaining these limits and this differentiated shape across individuals and time.

The invariability of the territories is also supported by the statistical results of the GLMM in the sense that the limits of the total home range size (K95%) do not vary significantly either over time or by the different occupants. Both the extension of active use areas (i.e. feeding and resting; K75%) and the core areas of the territory (K50%) are invariant between years and between individuals within the same territory. The smaller home range size of females (K95%, K75%, and K50%) is explained by incubation tasks during the breeding season (López-López et al. 2021).

### **Territory eccentricity**

The invariance in eccentricity within each territory corroborates the stability of territory physiognomy. Eccentricity has been previously studied in Bonelli's eagles between breeding and non-breeding periods (Bosch et al. 2010), finding a significant eccentricity value for breeding areas about the global home range. In other species such as the booted eagle (*Aquila pennata*), eccentricity has been also studied without finding differences between sexes and between breeding and non-breeding seasons (López-López et al. 2016a).

The location of the nest in the different topographies of the territories can also vary, either centrally or eccentrically. Despite these differences, the distance between the centroid and the nest remains constant among the different individuals occupying each territory over time. These results suggest that territory use is similar for different individuals regardless of nest location and the maintenance of territories independent of time and owners is once again reaffirmed.

### **Simple and double replacement cases**

To further demonstrate our hypothesis, we now discuss the cases of territories where single or double substitution occurred, which is a complementary step in the study of territorial stability. The members of the pairs occupying the territories in most cases of replacement had died or disappeared and the new member maintained the same territory as the previous one. How does the fact that both members of the pair disappear at the same time affect the physiognomy and boundaries of the territory?

Our hypothesis on the invariability of the territory is shown again. For example, in the first case of a double turnover, despite the disappearance of the pair, the neighbors did not occupy a part of the territory by extending the boundary of their territory in that direction. Instead, they maintained their boundaries with the same configuration and eccentricity. In a second case, two neighboring pairs did not extend their territorial boundaries into the territory of the pair that had disappeared. The pair that did so inhabited practically wholly of the new territory except for the most distant parts, maintaining their original territory with pre-existing boundaries in the occupied territory and did not extend the area of the occupied territory nor its shape. This could happen because the territory of the missing pair was surrounded by marked pairs except on one side, which overlooks an orange grove, and urban territories that were not occupied by any Bonelli's eagle pair. In successive years, this pair that occupied two territories gradually reduced its extension but maintained the core area of both territories, and the neighbors

did not occupy part of the abandoned territory. In the case of simple replacements, our results show that the new member of the pair adapts the limits of its home range to the previous one, also similar to the other member of the pair (the non-substituted one).

To date, it was thought that territory boundaries were maintained by pressure from neighbors (Fryxell and Lundberg 1997; Adams 2001; López-Sepulcre and Kokko 2005) and disappeared when the defending pair died, disfiguring the boundaries and shape of the territory, resulting in the eventual occupation by neighboring pairs. The boundaries of the territories of the pair inhabiting the empty territory would also be disfigured. The turnover events recorded in this study using accurate GPS/GSM telemetry have made it possible to assess the outcome of individual turnover from established territories in long-lived vertebrates. To the best of our knowledge, this is the first time the pre-existence of territories with their entity, regardless of the individuals that occupy them, has been supported by field information.

In many animal strategies, the evolution of territoriality reflects the balance between benefit and cost (Ord 2021). Species whose males use territories to monopolize access to females appear to incur higher costs than those that defend only food resources (Adams 2001; Ord 2021). On the other hand, Wilson (1975) considered that territory could change in time and space and that it may not be a fixed space. On the contrary, others argued that territories are fixed spaces (Brown 1975; Kauffmann 1983). We consider that the existence of stable territories regardless of the individuals occupying them may represent an evolutionary advantage that we could divide into the following points: 1) territoriality increases population stability and floating individuals form a buffer against fluctuations (López-Sepulcre and Kokko 2005); 2) the age and the quality of a territory (measured as reproductive success) are correlated (Ferrer and Bisson 2003). We, therefore, distinguish a constant struggle in the floating population to reach the best territories, usually replacing agonistically a member of the pair or, in the case of a natural loss, occupying the vacant territory as soon as possible. Our field



observations show that replacement after a vacancy takes place usually in less than a few weeks. In contrast, the formation of new territories by tracked animals has not been recorded throughout the study period. In this continuous struggle, the best specimens settle in the best territories, which are the ones that favor the continuity of the population. We have proposed this territorial strategy for Bonelli's eagles, it remains to be seen which other animal groups or species are also partially or adapted to this strategy.

### **Implications for conservation**

In the protection and conservation of sedentary raptors it is of great importance to know the totality of their home range, and not only the location of the nest to be effective. Our article demonstrates that these territories have fixed limits and extensions independently of the individuals that occupy them and they can even be empty and when they are used again these limits are maintained. Therefore, this new approach to the territoriality of Bonelli's eagles, which could even be extended to other raptors, could be a novel and very important tool for the design of areas to protect this species. If we add to this the fact that the protection of a top predator and umbrella species allows the protection of many other species, the value of this application for the design of protected areas increases. In addition, Bonelli's eagle is one of the key species used by administrations to grant the status of Special Protection Area for Birds (SPA). We believe that for designing new SPAs or redesigning currently declared SPAs, this new point of view can optimize the conservation of Bonelli's eagle and the conservation of the territory. In this way, the protected hectares would coincide exactly with the useful and occupied areas by this species regardless of population variations. Hence, the identification of territories, regardless of their state of occupation and conservation, will facilitate their occupation when an eventual recovery of the species occurs. Finally, this study highlights the role of modern telemetry techniques to better understand the exact delimitation of territories. This idea makes it possible to act with the greatest precision, for example, in the delimitation of protected areas or in carrying out management actions for endangered species.

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## CONCLUSIONES

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- 1) El territorio de un águila-azor perdicera en hábitats mediterráneos, medido con la mayor precisión hasta ahora utilizada, es de  $54,86 \pm 20,57$  km<sup>2</sup> de superficie. El territorio se mantiene constante todo el año sin diferencias entre el macho y la hembra de la pareja.
- 2) Los territorios de las parejas contiguas están claramente definidos y solo se produce un  $4,18 \pm 5,53$  % de solapamiento en sus límites.
- 3) Se ha demostrado que para conocer el área de campeo del águila real y del águila-azor perdicera, serían suficientes 15 días de seguimiento que corresponderían a unas 2800 localizaciones por satélite, con una frecuencia de una localización cada cinco minutos. Se pronostica que en el resto de rapaces territoriales no debe ser muy diferente.
- 4) Los incendios forestales no afectan al área de campeo ni a la reproducción del águila-azor perdicera cuando se producen en su territorio. No parece afectarles en absoluto excepto los primeros días del incendio, pudiendo ser por los disturbios provocados por los equipos de emergencia más que por el propio incendio.
- 5) Los límites y forma de los territorios del águila-azor perdicera se mantienen en el tiempo independientemente de los individuos que ocupan estos territorios y de otras circunstancias, abriendo un interesante campo de investigación sobre la territorialidad.
- 6) La estabilidad de la fisionomía de los territorios del águila-azor perdicera y su resiliencia a los incendios forestales muestran la perfecta adaptación a los ecosistemas mediterráneos.



## APÉNDICE I

Material suplementario del CAPÍTULO 1. Home-range size and space use of territorial Bonelli's Eagles (*Aquila fasciata*) tracked by high resolution GPS/GSM telemetry.

**Table S1** Summary information of the 51 Bonelli's eagles tracked by GPS/GSM satellite telemetry in eastern Spain.

Individual	Territory	Sex	Tagging date	End day of data transmission or data analysis	No. locations
Abel	1	Male	19/05/2015	02/09/2016	70,070
Adan	1	Male	31/01/2017	16/06/2020	202,346
Aura	1	Female	19/05/2015	21/05/2021	233,314
Berta	2	Female	10/06/2015	04/07/2015	4,366
Blas	2	Male	10/06/2015	27/06/2016	60,636
Boira	2	Female	06/11/2015	28/06/2016	26,501
Boj	2	Male	11/04/2017	19/06/2017	11,235
Bruma	2	Female	11/04/2017	21/05/2021	228,029
Carbo	3	Male	28/10/2015	25/03/2020	194,875
Carla	3	Female	28/10/2015	30/11/2018	105,168
Dino	4	Male	29/10/2015	21/03/2018	123,451
Dora	4	Female	29/10/2015	21/03/2018	135,077
Enebro	5	Male	07/06/2016	06/07/2020	219,785
Faig	6	Male	08/06/2016	21/05/2021	257,640
Fauna	6	Female	18/05/2017	21/05/2021	134,853
Flora	6	Female	08/06/2016	14/12/2016	26,633
Garra	7	Female	07/10/2016	24/02/2019	128,447
Gel	7	Male	07/10/2016	21/05/2021	234,500
Haeckel	8	Male	20/04/2017	01/04/2018	53,850
Helios	8	Male	06/10/2016	26/01/2017	14,033
Hydra	8	Female	06/10/2016	07/03/2018	74,598
Iris	9	Female	09/12/2016	27/03/2017	11,567

<b>Individual</b>	<b>Territory</b>	<b>Sex</b>	<b>Tagging date</b>	<b>End day of data transmission or data analysis</b>	<b>No. locations</b>
Isis	9	Male	09/12/2016	20/01/2017	4,352
Jara	10	Female	14/06/2017	21/05/2021	215,518
Juan	10	Male	05/06/2017	13/11/2020	164,822
Karma	11	Female	06/06/2017	29/03/2018	42,589
Koko	11	Male	13/09/2017	29/03/2018	26,490
Linneo	12	Male	11/07/2017	21/05/2021	217,907
Lucy	12	Female	11/07/2017	31/12/2019	108,127
Margulis	13	Female	06/06/2018	21/05/2021	156,689
Mendel	13	Male	06/06/2018	21/05/2021	173,427
Newton	14	Male	07/06/2018	31/03/2019	46,076
Nube	14	Female	06/06/2018	31/12/2018	34,708
Ochoa	15	Male	08/06/2018	21/05/2021	169,997
Olympia	15	Female	11/06/2018	21/05/2021	181,436
Pino	16	Male	23/06/2020	06/07/2020	1,016
Pluma	16	Female	28/01/2019	21/05/2021	55,635
Popper	16	Male	28/01/2019	16/10/2019	24,800
Rosalind	17	Female	03/06/2019	21/05/2021	43,955
Rutherford	17	Male	03/06/2019	21/05/2021	47,904
Sabina	18	Female	13/06/2019	21/02/2020	17,333
Salvia	18	Female	09/06/2020	21/05/2021	16,543
Sauce	18	Male	12/06/2019	21/05/2021	46,935
Taiga	19	Female	21/06/2019	21/05/2021	37,701
Tejo	19	Male	15/06/2019	21/05/2021	46,985
Ulex	20	Male	08/10/2019	31/12/2020	18,147
Uva	20	Female	08/10/2019	01/01/2021	17,727
Vera	21	Female	07/11/2019	21/05/2021	33,424
Verdi	21	Male	07/11/2019	21/05/2021	43,456
Villena Female	22	Female	17/05/2018	31/12/2019	77,923
Villena Male	22	Male	17/05/2018	21/05/2021	168,484

**Table S2** Summary statistics of daily home-range size (km<sup>2</sup>) per individual according to three different spatial estimators (i.e., K95%, K75% and K50%).

Individual	Territory	Count	K95 %		K75 %		K50 %	
			Mean	sd	Mean	sd	Mean	sd
Abel	1	471	43.395	47.510	18.422	16.327	8.307	7.536
Adan	1	1233	66.091	30.852	30.946	15.362	14.370	7.661
Aura	1	2091	54.255	45.832	24.498	20.482	11.120	9.712
Berta	2	26	51.02	31.939	21.986	13.934	10.076	6.526
Blas	2	384	40.174	37.932	16.358	14.764	7.269	6.587
Boira	2	225	28.576	32.807	11.777	14.767	5.237	6.896
Boj	2	64	43.774	34.008	18.767	14.162	8.693	6.657
Bruma	2	1417	44.546	52.184	17.804	18.223	7.882	7.858
Carbo	3	1608	54.514	42.297	23.610	17.820	10.672	8.344
Carla	3	777	50.018	37.346	21.694	17.278	9.686	8.016
Dino	4	805	49.670	22.164	22.639	11.500	10.248	5.654
Dora	4	875	41.344	26.916	18.191	13.391	8.159	6.377
Enebro	5	1491	55.802	55.802	24.064	18.623	10.906	8.783
Faig	6	1728	74.152	45.246	33.396	22.319	15.288	10.918
Fauna	6	1353	88.845	55.017	40.668	27.495	18.715	13.665
Flora	6	190	57.079	40.610	26.090	19.470	12.194	9.417
Garra	7	870	46.310	37.288	19.439	16.658	8.654	7.750
Gel	7	1623	51.922	35.989	22.026	16.558	9.786	7.808
Haeckel	8	346	33.634	23.892	13.803	9.263	6.235	4.260
Helios	8	113	28.549	18.421	12.796	8.739	5.789	4.096
Hydra	8	518	26.092	19.678	10.452	8.312	4.592	3.859
Iris	9	109	25.638	39.296	10.284	16.874	4.671	7.774
Isis	9	46	22.436	38.279	10.140	18.755	4.714	8.941
Jara	10	1347	35.313	22.431	15.239	9.698	6.898	4.604
Juan	10	1104	45.310	43.165	19.222	16.269	8.795	7.645
Karma	11	297	51.317	47.636	22.593	21.574	10.533	10.382
Koko	11	198	56.860	63.937	25.366	30.092	11.881	14.785
Linneo	12	1343	83.835	53.175	36.635	24.242	16.388	11.573
Lucy	12	839	84.428	121.653	37.260	60.360	16.644	28.069

Individual	Territory	Count	K95 %		K75 %		K50 %	
			Mean	sd	Mean	sd	Mean	sd
Margulis	13	951	53.009	39.655	23.524	18.337	10.849	8.931
Mendel	13	1013	56.498	30.099	25.371	14.804	11.646	7.247
Newton	14	298	88.771	80.323	38.958	36.567	17.869	17.141
Nube	14	208	78.713	76.146	33.419	36.339	15.053	17.484
Ochoa	15	1018	59.204	75.709	25.779	35.131	11.934	16.729
Olympia	15	1011	62.806	142.687	26.971	65.035	12.343	30.213
Pino	16	14	80.206	30.202	41.094	17.422	20.742	9.572
Pluma	16	691	35.723	32.428	16.015	14.322	7.432	6.948
Popper	16	232	51.428	41.383	22.711	18.865	10.429	8.685
Rosalind	17	560	25.524	22.142	11.085	9.299	5.124	4.427
Rutherford	17	559	27.298	20.835	12.183	9.805	5.659	4.866
Sabina	18	227	63.970	66.833	28.629	29.228	13.258	14.231
Salvia	18	220	71.536	63.769	32.325	30.010	15.094	14.423
Sauce	18	593	82.029	65.745	38.277	31.558	17.797	15.206
Taiga	19	572	35.502	57.337	14.893	17.241	6.810	7.697
Tejo	19	589	46.890	217.078	20.872	102.214	9.661	48.038
Ulex	20	396	116.106	214.752	56.422	108.062	27.323	54.364
Uva	20	396	95.413	181.324	47.788	99.890	23.093	50.092
Vera	21	385	45.181	37.823	19.846	16.618	9.064	7.937
Verdi	21	431	56.519	74.680	25.067	31.749	11.399	13.448
YHembra	22	535	57.245	56.452	21.720	22.900	9.250	10.257
YMacho	22	1050	73.442	381.809	30.025	188.364	13.243	90.580

**Table S3** ANOVA results of interannual variation in monthly average daily home range size according to 95% kernel by individual. Significant values are highlighted in bold.

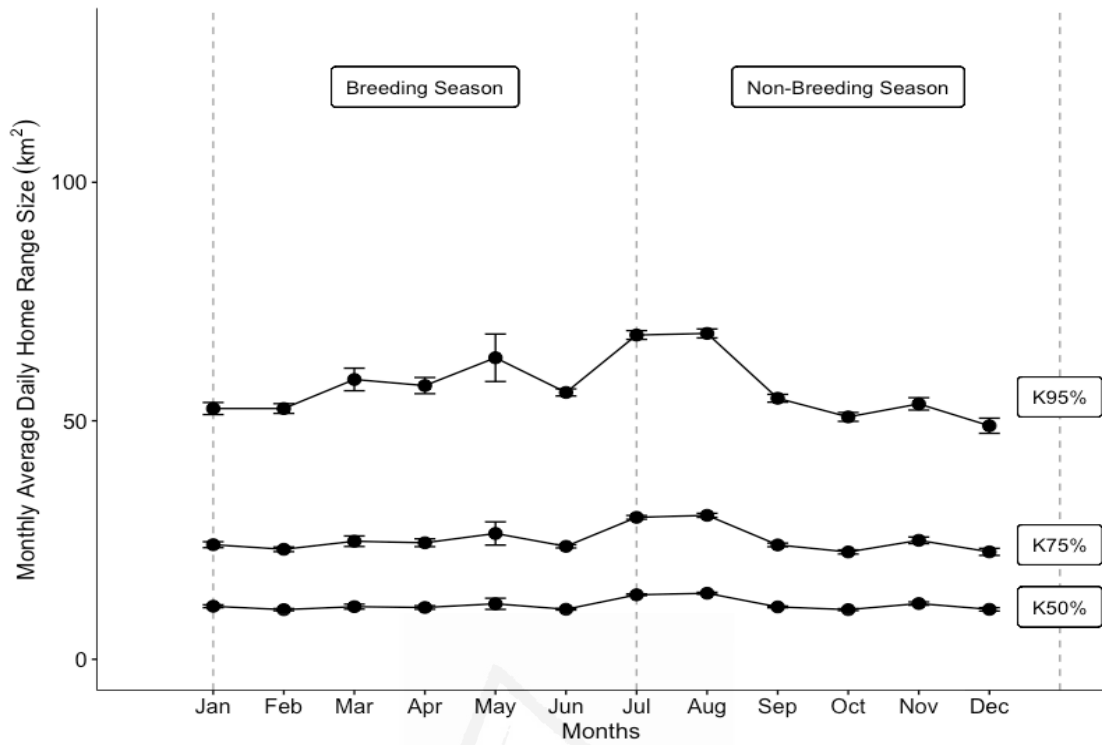
Individual	Variable	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Abel	year	1	0	0.4	0.001	0.973
	Residuals	14	4472	319.4		
Adan	year	3	10005	3335.0	19.180	< <b>0.001</b>
	Residuals	38	6607	174.0		
Aura	year	6	17914	2985.6	5.773	< <b>0.001</b>
	Residuals	65	33618	517.2		
Blas	year	1	64.6	64.6	0.483	0.500
	Residuals	12	1605.6	133.8		
Boira	year	1	473.6	473.6	1.661	0.245
	Residuals	6	1711.3	285.2		
Bruma	year	4	2360	589.9	1.962	0.118
	Residuals	43	12931	300.7		
Carbo	year	5	2570	514.0	2.517	<b>0.042</b>
	Residuals	48	9801	204.2		
Carla	year	3	680	226.7	0.817	0.496
	Residuals	26	7211	277.4		
Dino	year	3	2422	807.4	11.380	< <b>0.001</b>
	Residuals	25	1773	70.9		
Dora	year	3	4122	1374.2	5.103	<b>0.007</b>
	Residuals	26	7002	269.3		
Enebro	year	4	4174	1043.5	2.719	<b>0.041</b>
	Residuals	45	17268	383.7		
Faig	year	5	7513	1502.6	4.217	<b>0.003</b>
	Residuals	53	18886	356.3		
Fauna	year	4	7242	1810.6	5.700	<b>0.001</b>
	Residuals	42	13341	317.6		
Garra	year	3	2633	877.6	1.802	0.173
	Residuals	25	12178	487.1		
Gel	year	5	3549	709.9	1.953	0.103



Apéndice I

Individual	Variable	Df	Sum Sq	Mean Sq	F value	Pr(>F)
	Residuals	48	17444	363.4		
Haeckel	year	1	354.6	354.6	1.491	0.248
	Residuals	11	2615.5	237.8		
Helios	year	1	5.95	6.0	0.083	0.801
	Residuals	2	143.97	72.0		
Hydra	year	2	271	135.5	1.516	0.249
	Residuals	16	1430	89.4		
Iris	year	1	14.43	14.4	0.119	0.763
	Residuals	2	242.61	121.3		
Jara	year	4	1474	368.4	3.497	<b>0.015</b>
	Residuals	41	4319	105.3		
Juan	year	3	3231	1076.9	6.217	<b>0.002</b>
	Residuals	35	6062	173.2		
Koko	year	1	3058.4	3058.4	19.380	<b>0.007</b>
	Residuals	5	789.1	157.8		
Karma	year	1	45.4	45.4	0.153	0.706
	Residuals	8	2377.7	297.2		
Linneo	year	4	2162	540.5	2.544	0.054
	Residuals	40	8499	212.5		
Lucy	year	2	6957	3479.0	3.505	<b>0.044</b>
	Residuals	27	26798	993.0		
Margulis	year	3	198	66.0	0.147	0.931
	Residuals	30	13438	447.9		
Mendel	year	3	559	186.4	1.013	0.401
	Residuals	30	5520	184.0		
Newton	year	1	1119	1119.0	3.031	0.120
	Residuals	8	2953	369.1		
Ochoa	year	3	7675	2558.0	3.068	<b>0.043</b>
	Residuals	30	25019	834.0		
Olympia	year	3	18026	6009.0	2.380	0.089
	Residuals	30	75725	2524.0		
Pluma	year	2	223	111.7	0.488	0.620

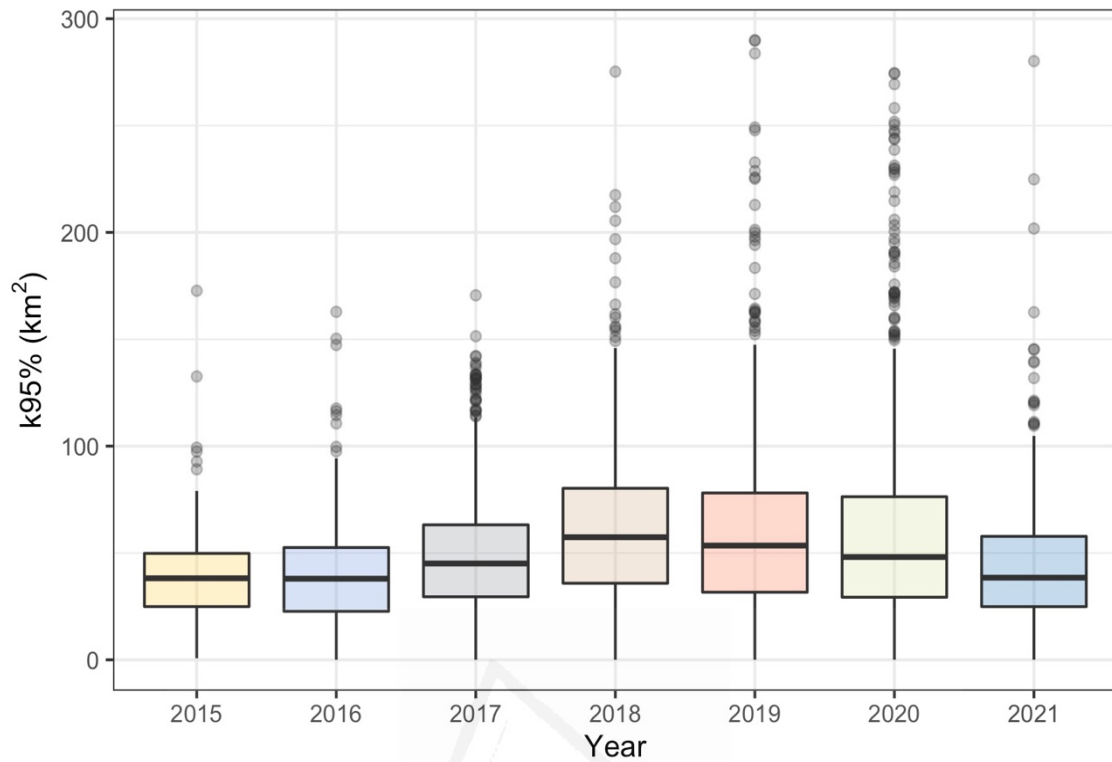
Individual	Variable	Df	Sum Sq	Mean Sq	F value	Pr(>F)
	Residuals	25	5721	228.8		
Rosalind	year	2	15.4	7.7	0.087	0.917
	Residuals	19	1672.2	88.0		
Rutherford	year	2	57.8	28.9	0.537	0.593
	Residuals	19	1022.5	53.8		
Sabina	year	1	4118	4118.0	3.374	0.109
	Residuals	7	8543	1220.0		
Sauce	year	2	2321	1160.0	0.899	0.423
	Residuals	20	25814	1291.0		
Salvia	year	1	3553	3553.0	2.907	0.132
	Residuals	7	8556	1222.0		
Taiga	year	2	663	331.5	1.082	0.359
	Residuals	19	5824	306.5		
Tejo	year	2	2541	1270.0	0.595	0.561
	Residuals	19	40548	2134.0		
Ulex	year	1	6767	6767.0	0.664	0.430
	Residuals	13	132535	10195.0		
Uva	year	1	71745	71745.0	29.310	< 0.001
	Residuals	13	31821	2448.0		
Vera	year	2	1160	579.9	3.626	0.054
	Residuals	14	2239	159.9		
Verdi	year	2	1237	618.3	1.584	0.240
	Residuals	14	5464	390.3		
Villena Female	year	1	671	671.3	0.728	0.405
	Residuals	17	15668	921.6		
Villena Male	year	3	32495	10832.0	0.931	0.437
	Residuals	32	372154	11630.0		



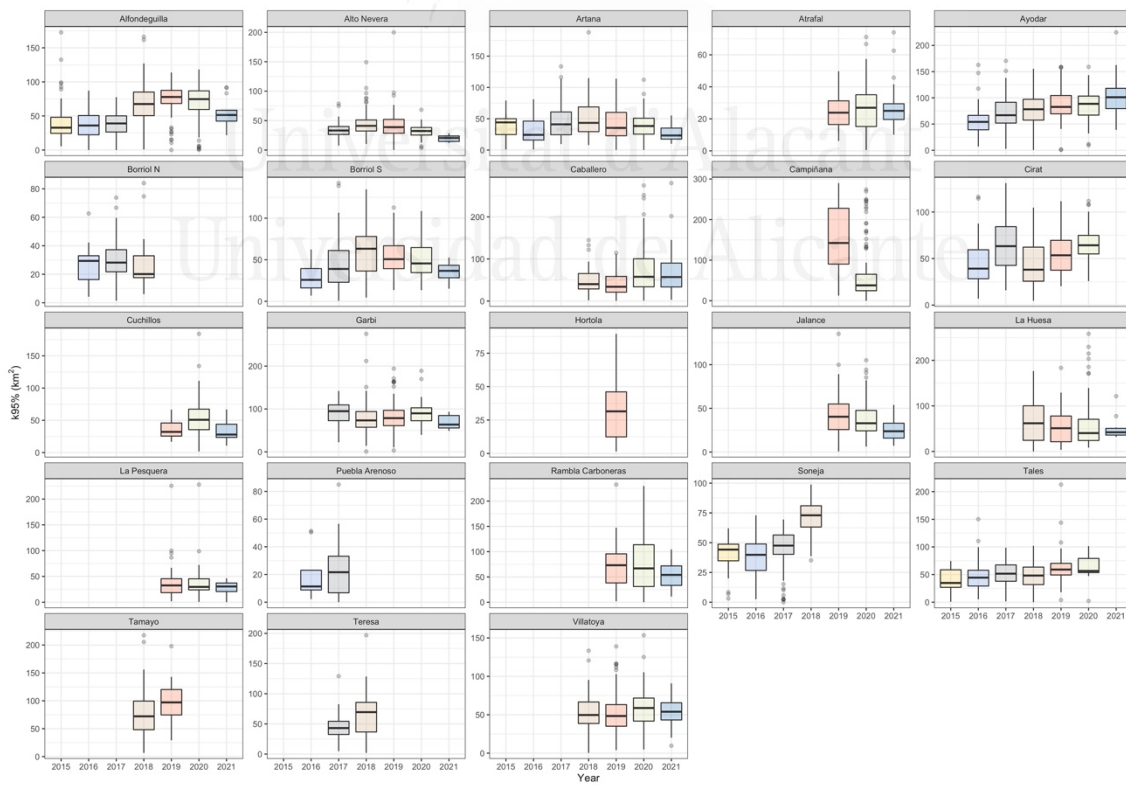
**Figure S1** Monthly average of the daily home range size at three different levels (K95%, K75% and K50%).



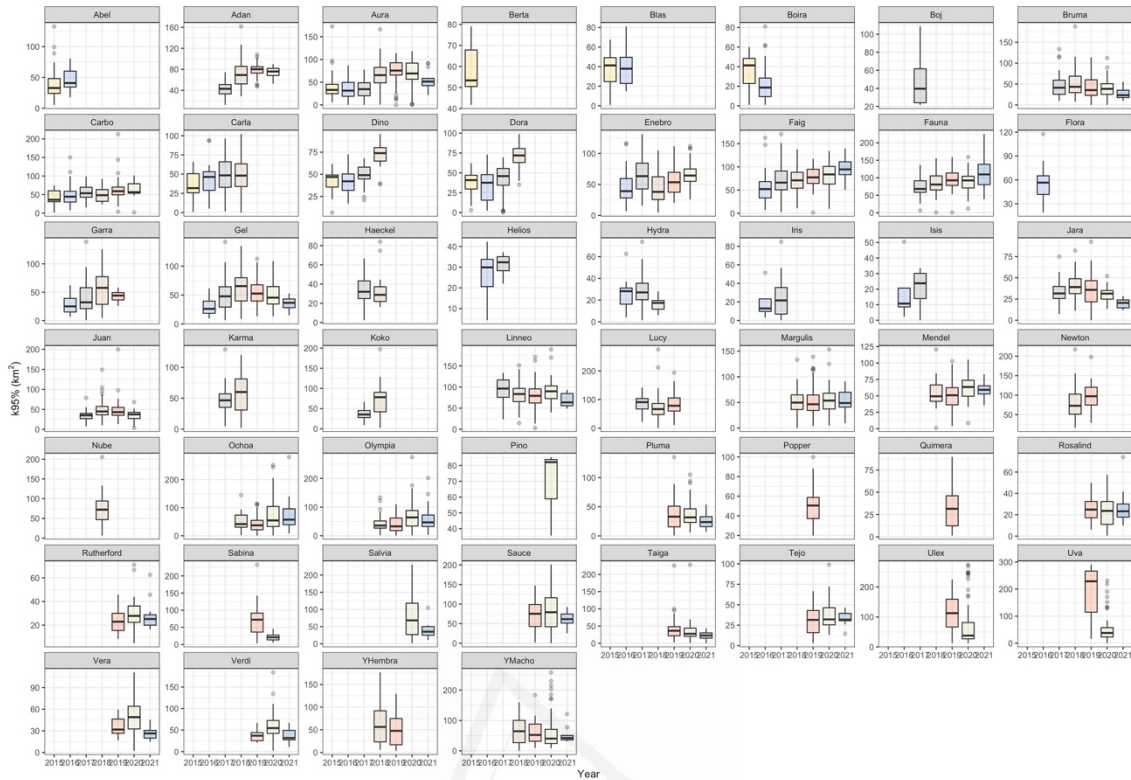
**Figure S2** Boxplot of the monthly average of the daily home range size (K95%) per territory.



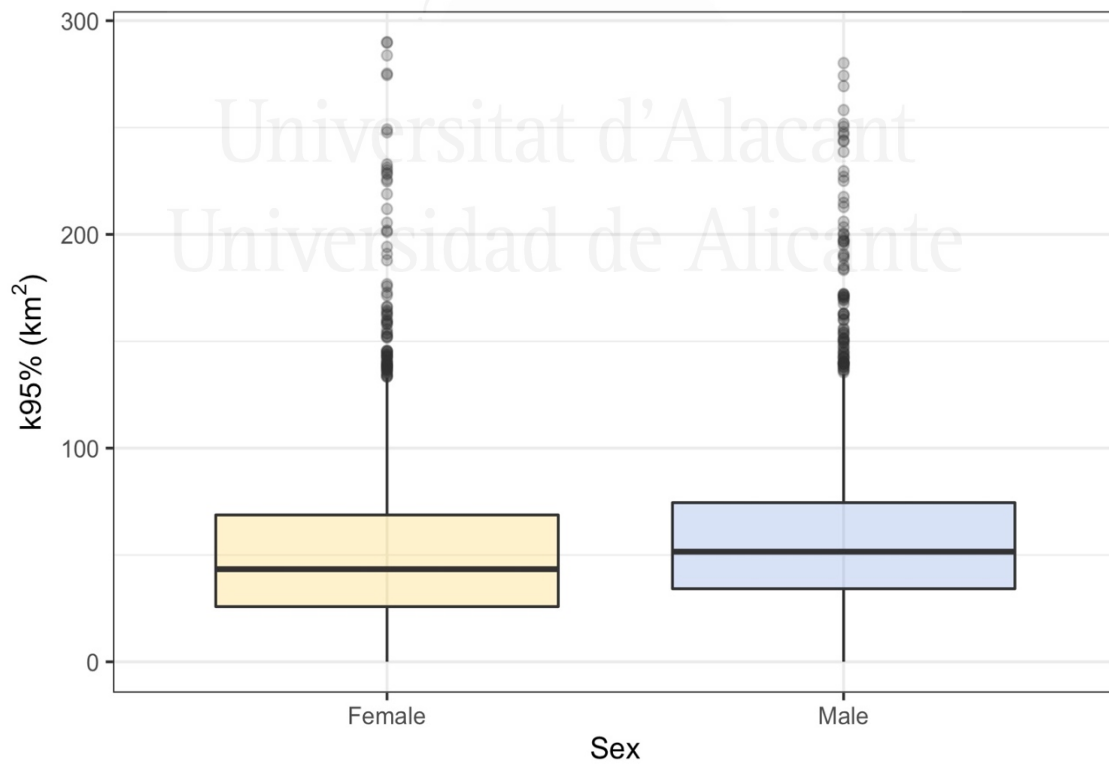
**Figure S3** Differences in daily home range size (K95%) among years.



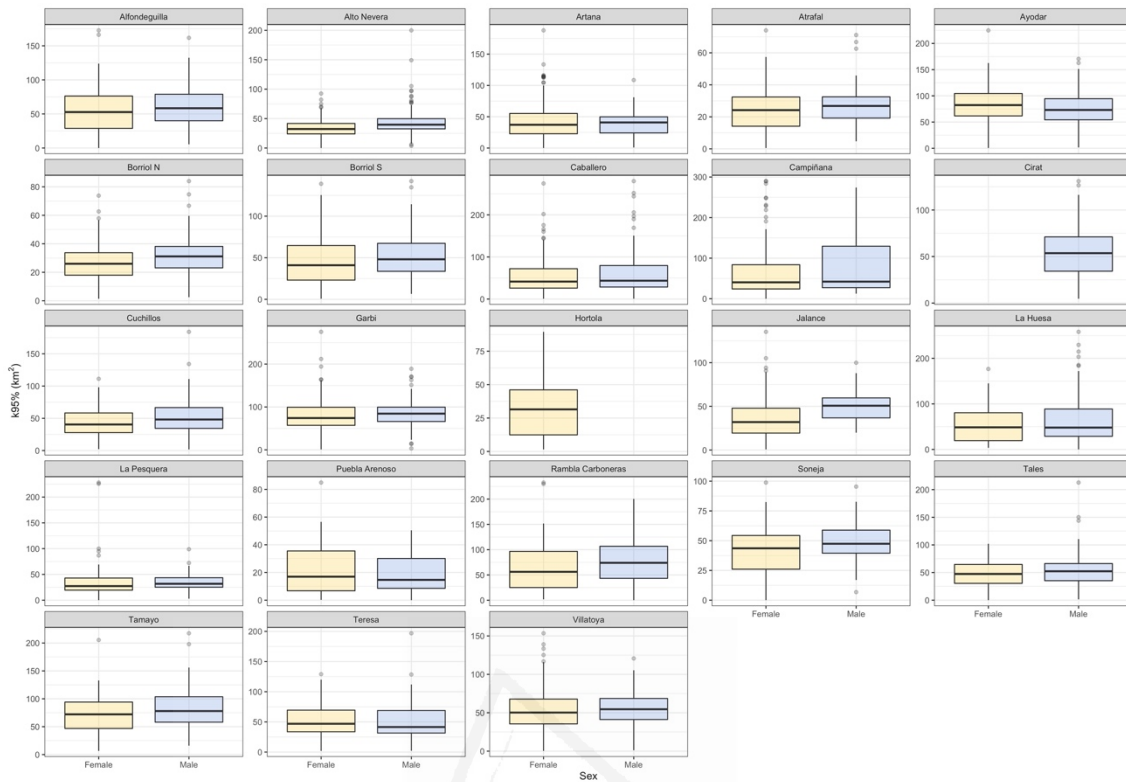
**Figure S4** Differences in daily home range size (K95%) among years and territories.



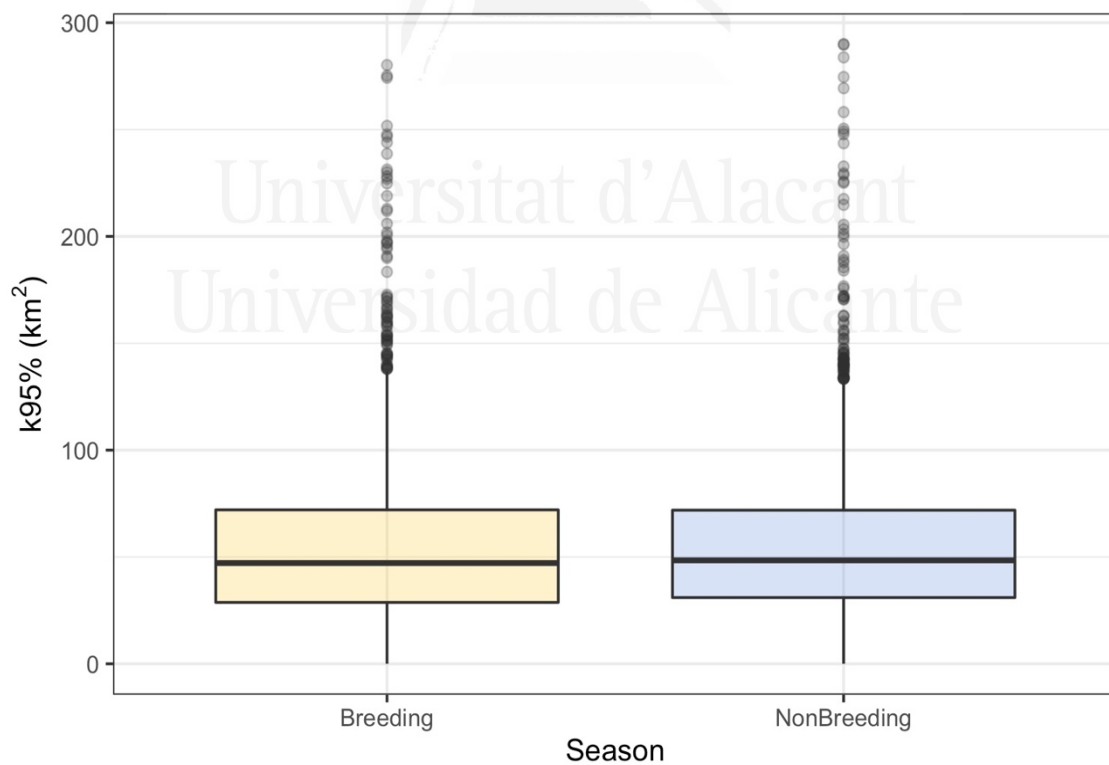
**Figure S5** Differences in daily home range size (K95%) among years per individual.



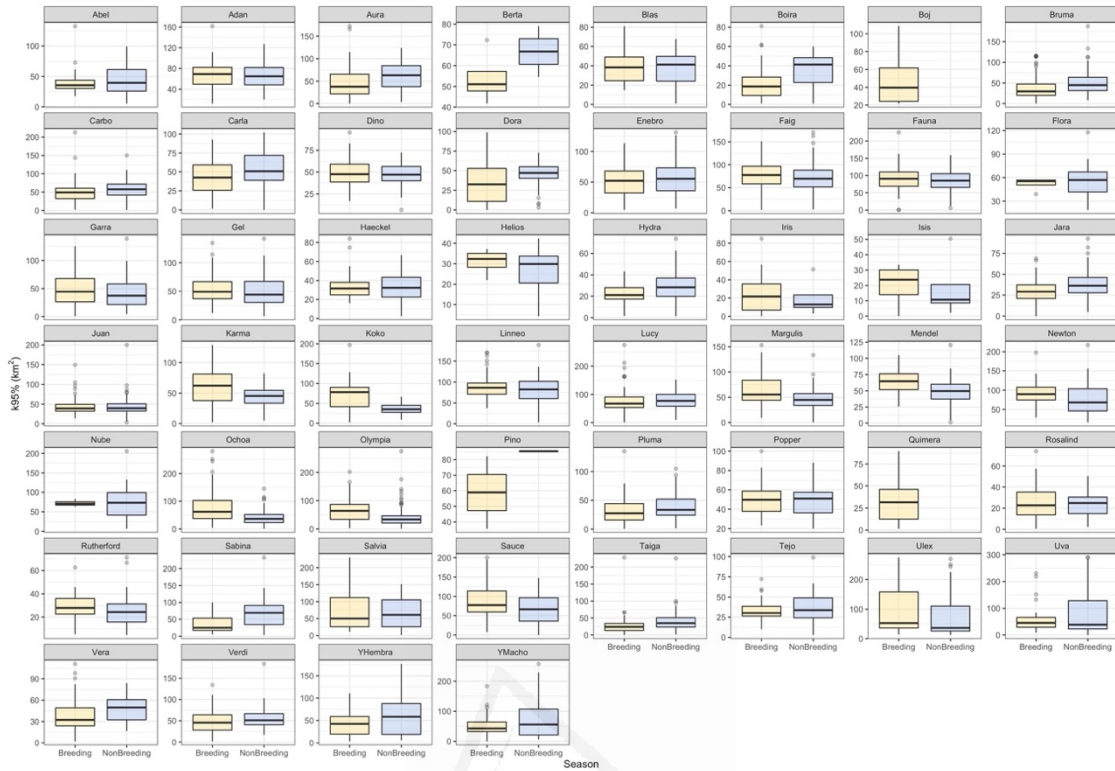
**Figure S6** Differences in the daily home range size (K95%) between sexes.



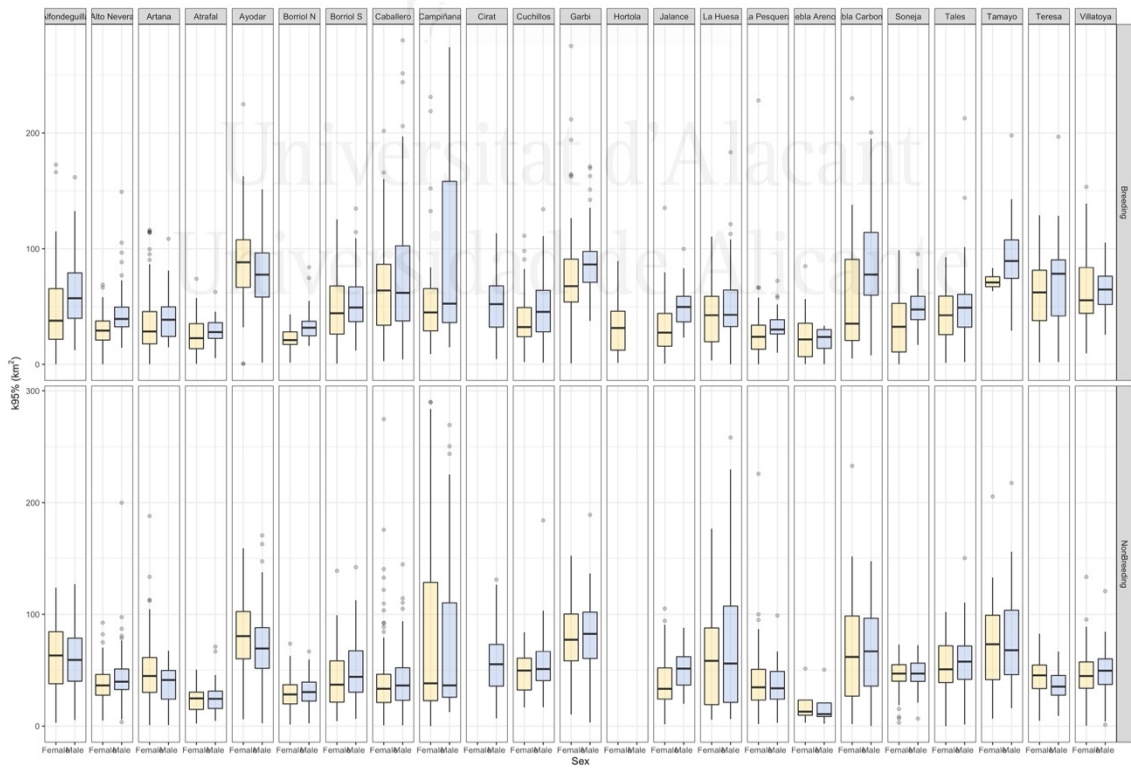
**Figure S7** Differences in daily home range size (K95%) between sexes and territories.



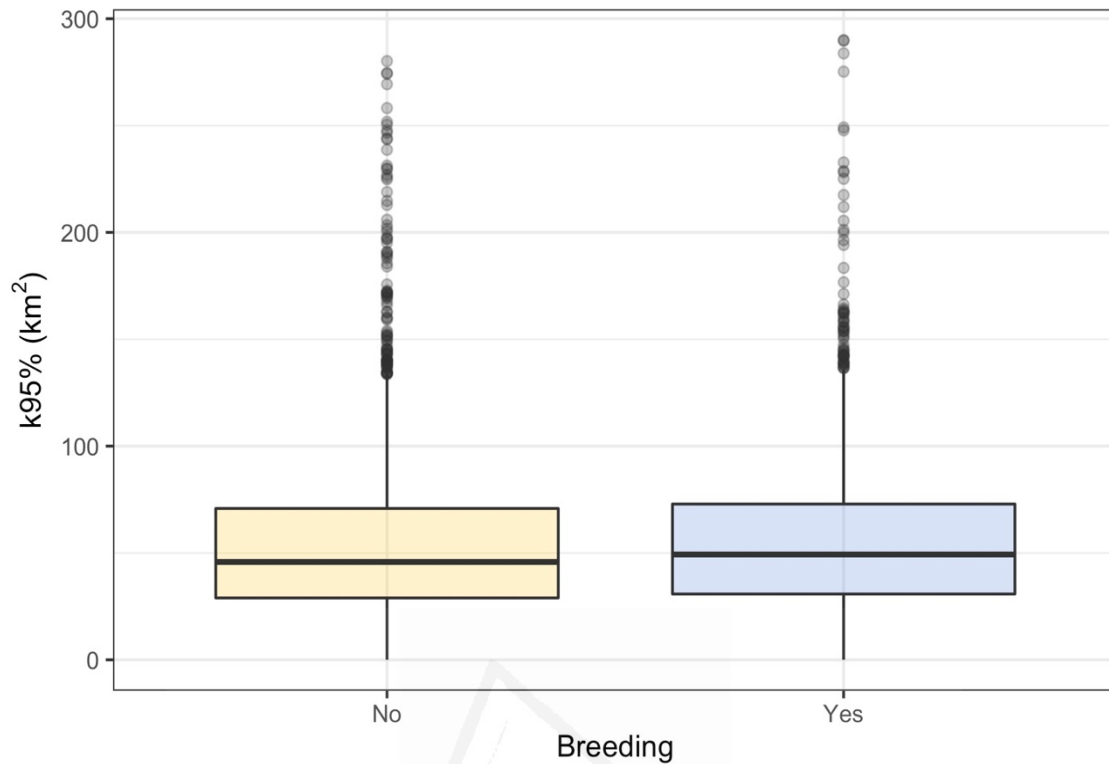
**Figure S8** Differences in the daily home range size (K95%) between seasons.



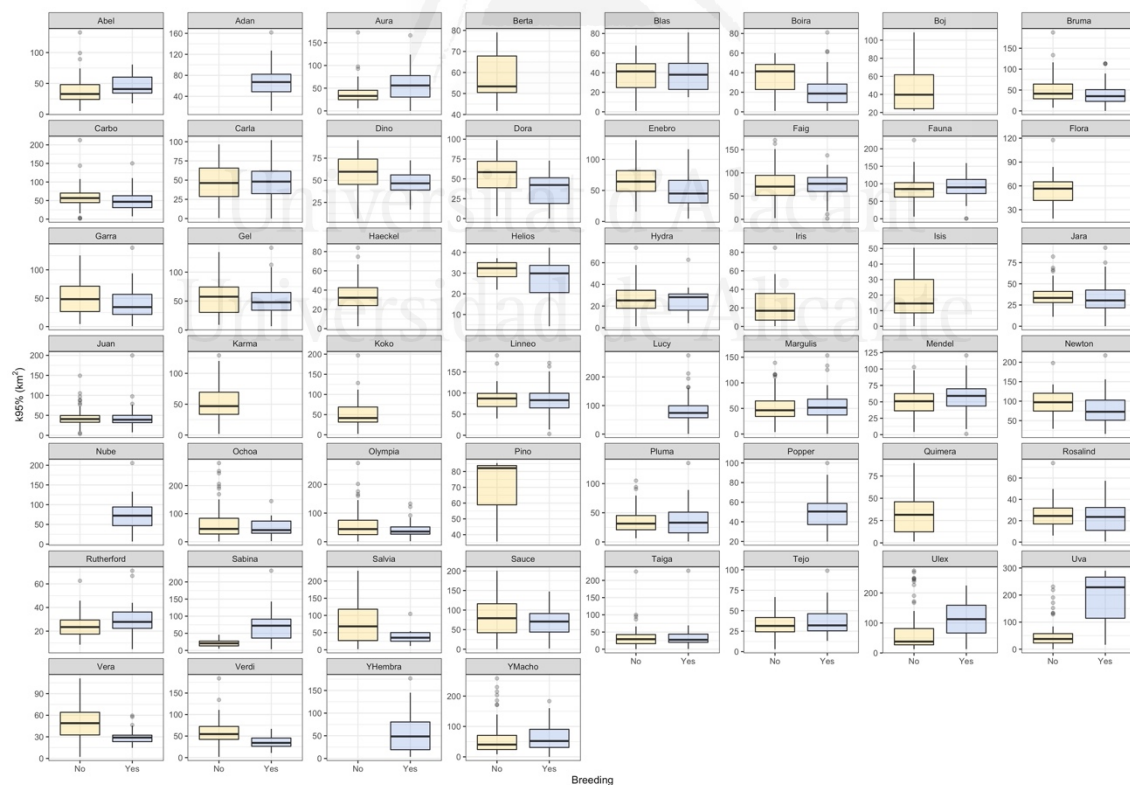
**Figure S9** Differences in daily home range size (K95%) between seasons and territories.



**Figure S10** Differences in daily home range size (K95%) between sexes, season and territories.



**Figure S11** Differences in daily home range size (K95%) between breeding status.



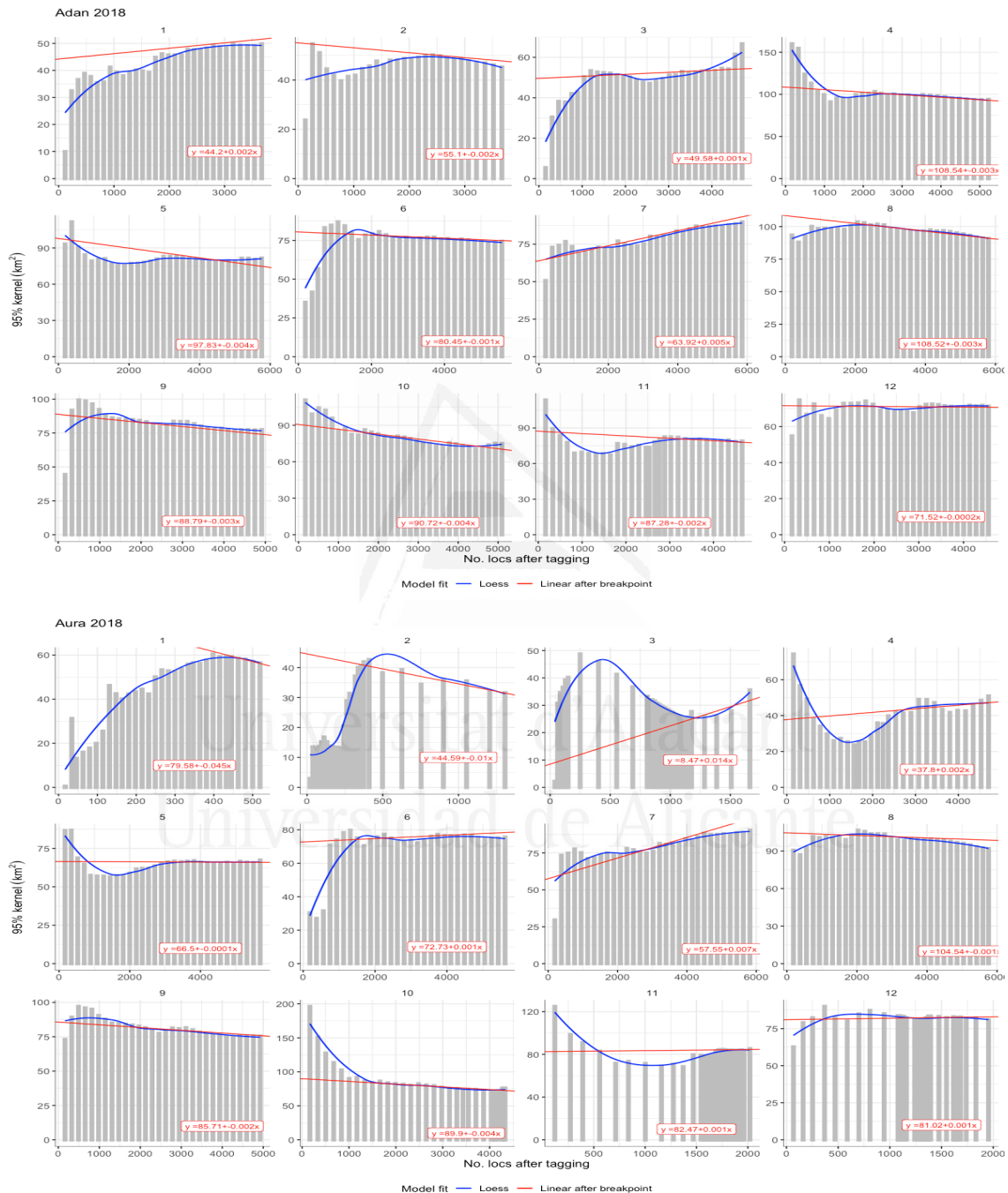
**Figure S12** Differences in daily home range size (K95%) between breeding status and individuals.



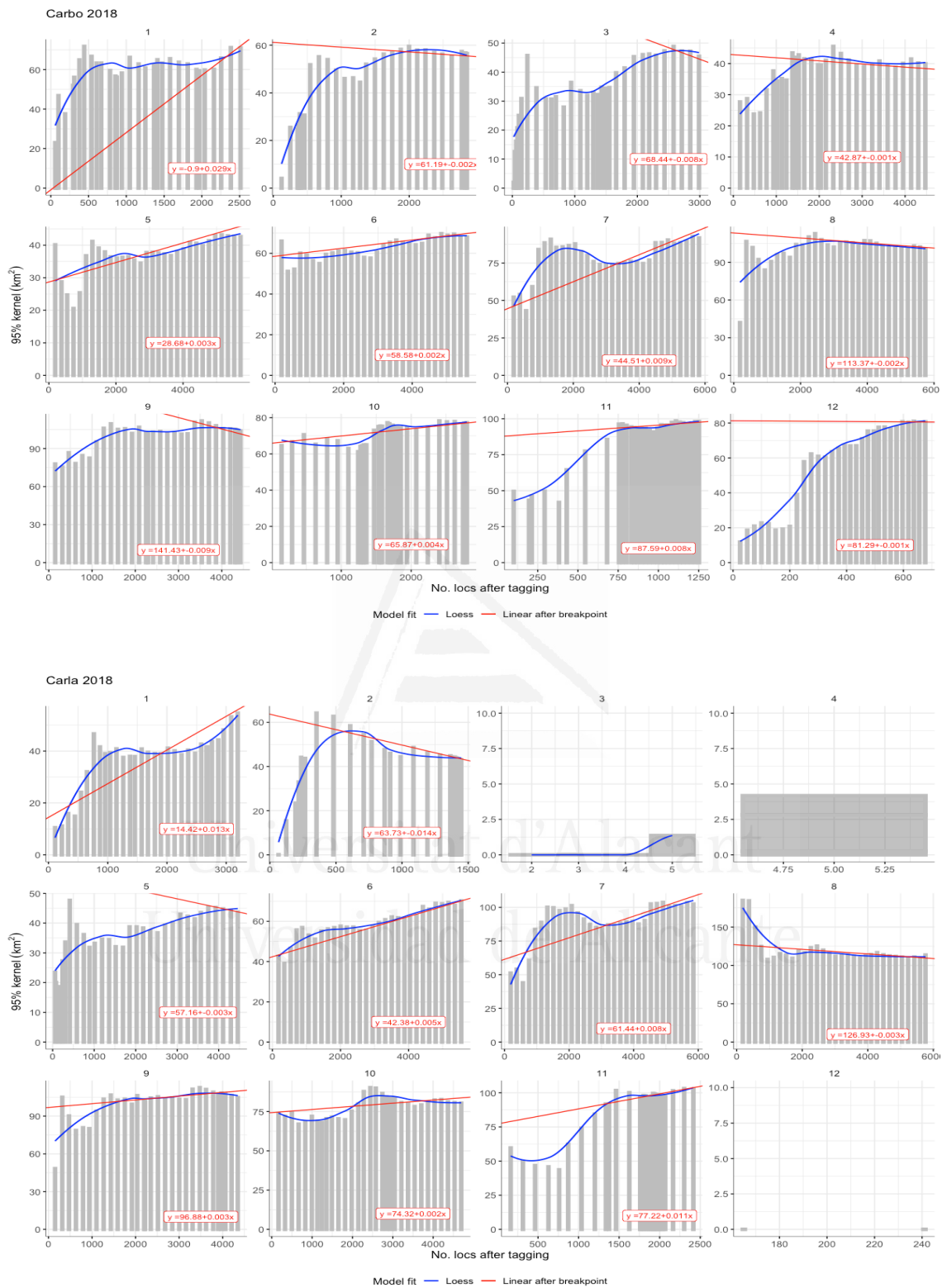


# APÉNDICE II

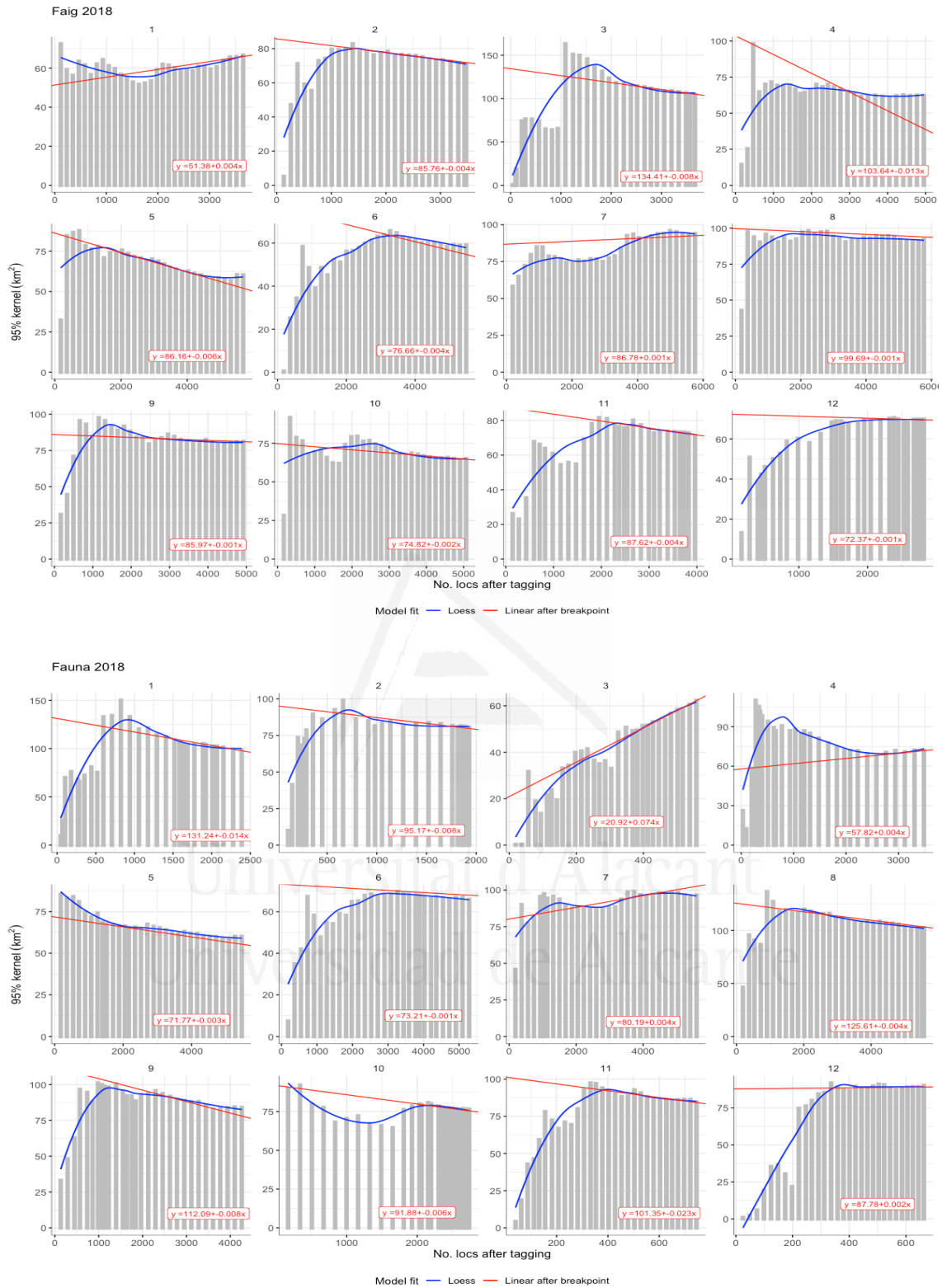
Material suplementario del CAPÍTULO 2. Fifteen days are enough to estimate home-range size in some long-lived resident eagles.



**Figure S1** Accumulation daily 95% kernel surface during every 2018's month of Adan and Aura. Linear regression fit after the breakpoint (red line) and smoothed fitting line (blue line) are shown.



**Figure S2** Accumulation daily 95% kernel surface during every 2018's month of Carbo and Carla. Linear regression fit after the breakpoint (red line) and smoothed fitting line (blue line) are shown.



**Figure S3** Accumulation daily 95% kernel surface during every 2018's month of Faig and Fauna. Linear regression fit after the breakpoint (red line) and smoothed fitting line (blue line) are shown.

**Table S1** Table results of the accumulation daily 95% kernel surface by individual.

ID	Species	Sex	Break point	SE	Intercept	Slop	Formula
Abel	A. fasciata	male	2580.24	532.36	63.83	-0.0039	$y = -0.0039 + 63.8x$
Adan	A. fasciata	male	2434.58	386.81	37.82	0.0017	$y = 0.0017 + 37.8x$
Aura	A. fasciata	female	2434.49	757.87	72.24	-0.0052	$y = -0.0052 + 72.2x$
Berta	A. fasciata	female	2605.74	257.54	47.45	0.0018	$y = 0.0018 + 47.5x$
Blas	A. fasciata	male	1536.18	147.10	49.35	0.0001	$y = 0.0001 + 49.3x$
Boira	A. fasciata	female	3138.16	249.91	95.04	-0.0085	$y = -0.0085 + 95x$
Bruma	A. fasciata	female	2423.29	195.52	106.46	-0.0099	$y = -0.0099 + 106.5x$
Carbo	A. fasciata	male	1543.86	165.14	87.02	0.001	$y = 0.001 + 87x$
Carla	A. fasciata	female	1433.99	3277.13	76.21	0.0038	$y = 0.0038 + 76.2x$
Dino	A. fasciata	male	1637.60	333.51	64.47	-0.0032	$y = -0.0032 + 64.5x$
Dora	A. fasciata	female	1852.30	592.39	63.63	-0.0032	$y = -0.0032 + 63.6x$
Enebro	A. fasciata	male	3403.23	311.54	61.18	-0.0017	$y = -0.0017 + 61.2x$
Faig	A. fasciata	male	2121.56	1076.59	75.17	-0.0046	$y = -0.0046 + 75.2x$
Fauna	A. fasciata	female	1952.28	1309.65	112.74	-0.0032	$y = -0.0032 + 112.7x$
Flora	A. fasciata	female	3902.21	256.60	55.01	0.0001	$y = 0.0001 + 55x$
Garra	A. fasciata	female	3442.00	1291.54	47.94	0.0012	$y = 0.0012 + 47.9x$
Female Villena	A. fasciata	female	2069.68	83.26	48.07	0.00004	$y = 0.00004 + 48.1x$
Gel	A. fasciata	male	2711.29	134.19	58.33	-0.0009	$y = -0.0009 + 58.3x$
Haeckel	A. fasciata	male	1235.92	56.20	36.75	0.0004	$y = 0.0004 + 36.8x$
Helios	A. fasciata	male	2556.26	228.02	36.09	0.0012	$y = 0.0012 + 36.1x$
Hydra	A. fasciata	female	2834.57	336.71	41.36	0.0003	$y = 0.0003 + 41.4x$
Isis	A. fasciata	male	2662.89	96.78	65.68	-0.0067	$y = -0.0067 + 65.7x$
Jara	A. fasciata	female	2120.57	675.74	34.64	-0.0004	$y = -0.0004 + 34.6x$
Juan	A. fasciata	male	3133.28	41.61	39.05	-0.0009	$y = -0.0009 + 39x$
Karma	A. fasciata	female	4240.91	271.76	98.25	-0.0038	$y = -0.0038 + 98.3x$
Koko	A. fasciata	male	3071.15	324.35	44.45	0.001	$y = 0.001 + 44.4x$
Linneo	A. fasciata	male	1803.25	204.38	156.35	-0.001	$y = -0.001 + 156.3x$
Lucy	A. fasciata	female	1756.98	198.38	152.65	-0.0015	$y = -0.0015 + 152.6x$
Male Villena	A. fasciata	male	4144.07	658.31	46.07	0.0041	$y = 0.0041 + 46.1x$
Margulis	A. fasciata	female	2545.01	365.77	42.62	0.0048	$y = 0.0048 + 42.6x$

ID	Species	Sex	Break point	SE	Intercept	Slop	Formula
Mendel	A. fasciata	male	2653.70	115.69	44.42	0.004	$y = 0.004 + 44.4x$
Newton	A. fasciata	male	3665.89	204.34	104.72	-0.0046	$y = -0.0046 + 104.7x$
Nube	A. fasciata	female	3374.87	159.65	89.37	-0.001	$y = -0.001 + 89.4x$
Ochoa	A. fasciata	male	1916.98	1350.68	30.84	0.0021	$y = 0.0021 + 30.8x$
Olympia	A. fasciata	female	3575.02	648.31	44.71	-0.0005	$y = -0.0005 + 44.7x$
Pino	A. fasciata	male	399.33	65.86	84.05	-0.0069	$y = -0.0069 + 84x$
Pluma	A. fasciata	female	1390.13	95.71	50.14	-0.0005	$y = -0.0005 + 50.1x$
Popper	A. fasciata	male	1230.55	64.24	58.73	-0.0022	$y = -0.0022 + 58.7x$
Quimera	A. fasciata	female	507.07	153.18	91.44	-0.0178	$y = -0.0178 + 91.4x$
Rosalind	A. fasciata	female	1786.25	92.29	37.90	-0.001	$y = -0.001 + 37.9x$
Rutherford	A. fasciata	male	2139.00	124.54	40.52	-0.002	$y = -0.002 + 40.5x$
Sabina	A. fasciata	female	459.24	35.96	96.56	-0.0001	$y = -0.0001 + 96.6x$
Salvia	A. fasciata	female	1361.28	88.86	157.30	0.003	$y = 0.003 + 157.3x$
Sauce	A. fasciata	male	466.18	22.55	109.06	0.0007	$y = 0.0007 + 109.1x$
Taiga	A. fasciata	female	2787.59	75.18	-8.89	0.0174	$y = 0.0174 - 8.9x$
Tejo	A. fasciata	male	2590.45	94.52	26.54	0.0011	$y = 0.0011 + 26.5x$
Ulex	A. fasciata	male	985.24	29.65	304.30	-0.1615	$y = -0.1615 + 304.3x$
Uva	A. fasciata	female	678.00	12.06	84.66	0.1435	$y = 0.1435 + 84.7x$
Vera	A. fasciata	female	1232.11	181.83	46.64	0.0024	$y = 0.0024 + 46.6x$
Verdi	A. fasciata	male	1941.17	172.55	58.18	-0.0031	$y = -0.0031 + 58.2x$
Carlos	A. chrysaetos	male	1712.56	101.27	44.88	-0.0029	$y = -0.0029 + 44.9x$
Clara	A. chrysaetos	female	1909.48	124.54	68.85	-0.0018	$y = -0.0018 + 68.8x$
Delta	A. chrysaetos	female	4574.43	240.93	31.70	-0.0004	$y = -0.0004 + 31.7x$
Einstein	A. chrysaetos	male	3814.79	211.21	88.07	-0.0001	$y = -0.0001 + 88.1x$
Gaia	A. chrysaetos	female	2997.50	115.71	33.17	0.0002	$y = 0.0002 + 33.2x$
Galileo	A. chrysaetos	male	2926.25	221.64	48.41	0.0127	$y = 0.0127 + 48.4x$
Hipatia	A. chrysaetos	female	1845.57	176.25	37.17	0.0008	$y = 0.0008 + 37.2x$
Icaro	A. chrysaetos	male	3033.37	170.99	81.38	-0.0027	$y = -0.0027 + 81.4x$
Jupiter	A. chrysaetos	male	2336.89	137.07	64.22	0.0116	$y = 0.0116 + 64.2x$

**Table S2** Table results of the accumulation daily 95% kernel surface month by month of the six individuals

ID	Month	Sex	No locs to breakpoint	SE	Intercept	Slope	Formula
Adan	January	male	2272.03	164.59	44.20	0.002	$y = 44.2 + 0.002x$
Adan	February	male	1976.32	77.71	55.10	-0.002	$y = 55.1 + -0.002x$
Adan	March	male	1155.26	114.02	49.58	0.001	$y = 49.58 + 0.001x$
Adan	April	male	2194.34	174.10	108.54	-0.003	$y = 108.54 + -0.003x$
Adan	May	male	3311.29	425.43	97.83	-0.004	$y = 97.83 + -0.004x$
Adan	June	male	1495.54	128.96	80.45	-0.001	$y = 80.45 + -0.001x$
Adan	July	male	1239.45	121.79	63.92	0.005	$y = 63.92 + 0.005x$
Adan	August	male	2218.99	257.27	108.52	-0.003	$y = 108.52 + -0.003x$
Adan	September	male	1364.52	81.26	88.79	-0.003	$y = 88.79 + -0.003x$
Adan	October	male	1238.52	116.74	90.72	-0.004	$y = 90.72 + -0.004x$
Adan	November	male	3044.32	249.52	87.28	-0.002	$y = 87.28 + -0.002x$
Adan	December	male	1222.70	152.21	71.52	-0.0002	$y = 71.52 + -0.0002x$
Aura	January	female	472.82	400.12	79.58	-0.045	$y = 79.58 + -0.045x$
Aura	February	female	332.43	7.67	44.59	-0.01	$y = 44.59 + -0.01x$
Aura	March	female	1112.37	18.13	8.47	0.014	$y = 8.47 + 0.014x$
Aura	April	female	2516.15	139.19	37.80	0.002	$y = 37.8 + 0.002x$
Aura	May	female	3051.64	230.54	66.50	-0.0001	$y = 66.5 + -0.0001x$
Aura	June	female	1688.85	322.95	72.73	0.001	$y = 72.73 + 0.001x$
Aura	July	female	2729.03	263.83	57.55	0.007	$y = 57.55 + 0.007x$
Aura	August	female	1030.29	115.42	104.54	-0.001	$y = 104.54 + -0.001x$
Aura	September	female	2289.99	474.78	85.71	-0.002	$y = 85.71 + -0.002x$
Aura	October	female	2115.50	464.34	89.90	-0.004	$y = 89.9 + -0.004x$
Aura	November	female	1748.26	46.10	82.47	0.001	$y = 82.47 + 0.001x$
Aura	December	female	1191.06	134.11	81.02	0.001	$y = 81.02 + 0.001x$
Carbo	January	male	2160.01	152.30	-0.90	0.029	$y = -0.9 + 0.029x$
Carbo	February	male	1683.23	126.74	61.19	-0.002	$y = 61.19 + -0.002x$
Carbo	March	male	2571.80	141.11	68.44	-0.008	$y = 68.44 + -0.008x$
Carbo	April	male	1470.33	119.54	42.87	-0.001	$y = 42.87 + -0.001x$
Carbo	May	male	2495.75	290.97	28.68	0.003	$y = 28.68 + 0.003x$
Carbo	June	male	3192.42	237.41	58.58	0.002	$y = 58.58 + 0.002x$
Carbo	July	male	3264.16	137.55	44.51	0.009	$y = 44.51 + 0.009x$
Carbo	August	male	2247.00	123.07	113.37	-0.002	$y = 113.37 + -0.002x$
Carbo	September	male	3403.52	52.02	141.43	-0.009	$y = 141.43 + -0.009x$
Carbo	October	male	1873.07	108.52	65.87	0.004	$y = 65.87 + 0.004x$
Carbo	November	male	705.99	30.16	87.59	0.008	$y = 87.59 + 0.008x$
Carbo	December	male	590.03	96.76	81.29	-0.001	$y = 81.29 + -0.001x$

ID	Month	Sex	No locs to breakpoint	SE	Intercept	Slope	Formula
Carla	January	female	2461.02	243.44	14.42	0.013	$y = 14.42 + 0.013x$
Carla	February	female	1124.47	169.67	63.73	-0.014	$y = 63.73 - 0.014x$
Carla	March	female	NA	NA	NA	NA	NA
Carla	April	female	NA	NA	NA	NA	NA
Carla	May	female	3967.30	608.33	57.16	-0.003	$y = 57.16 - 0.003x$
Carla	June	female	2754.00	453.42	42.38	0.005	$y = 42.38 + 0.005x$
Carla	July	female	2879.44	183.62	61.44	0.008	$y = 61.44 + 0.008x$
Carla	August	female	2262.00	375.59	126.93	-0.003	$y = 126.93 - 0.003x$
Carla	September	female	1431.87	411.27	96.88	0.003	$y = 96.88 + 0.003x$
Carla	October	female	3289.78	121.16	74.32	0.002	$y = 74.32 + 0.002x$
Carla	November	female	1838.42	84.36	77.22	0.011	$y = 77.22 + 0.011x$
Carla	December	female	NA	NA	NA	NA	NA
Faig	January	male	2065.48	396.27	51.38	0.004	$y = 51.38 + 0.004x$
Faig	February	male	1200.34	118.22	85.76	-0.004	$y = 85.76 - 0.004x$
Faig	March	male	2105.30	438.93	134.41	-0.008	$y = 134.41 - 0.008x$
Faig	April	male	3080.85	810.73	103.64	-0.013	$y = 103.64 - 0.013x$
Faig	May	male	2028.05	306.24	86.16	-0.006	$y = 86.16 - 0.006x$
Faig	June	male	3179.57	137.82	76.66	-0.004	$y = 76.66 - 0.004x$
Faig	July	male	3677.00	39.62	86.78	0.001	$y = 86.78 + 0.001x$
Faig	August	male	2123.59	201.12	99.69	-0.001	$y = 99.69 - 0.001x$
Faig	September	male	2169.07	171.97	85.97	-0.001	$y = 85.97 - 0.001x$
Faig	October	male	3103.02	201.87	74.82	-0.002	$y = 74.82 - 0.002x$
Faig	November	male	1863.92	81.15	87.62	-0.004	$y = 87.62 - 0.004x$
Faig	December	male	1981.01	317.74	72.37	-0.001	$y = 72.37 - 0.001x$
Fauna	January	female	1986.50	1475.05	131.24	-0.014	$y = 131.24 - 0.014x$
Fauna	February	female	1573.94	536.71	95.17	-0.008	$y = 95.17 - 0.008x$
Fauna	March	female	397.62	817.60	20.92	0.074	$y = 20.92 + 0.074x$
Fauna	April	female	2561.15	1031.51	57.82	0.004	$y = 57.82 + 0.004x$
Fauna	May	female	1502.45	98.91	71.77	-0.003	$y = 71.77 - 0.003x$
Fauna	June	female	3026.87	419.29	73.21	-0.001	$y = 73.21 - 0.001x$
Fauna	July	female	1957.36	379.55	80.19	0.004	$y = 80.19 + 0.004x$
Fauna	August	female	1289.90	399.40	125.61	-0.004	$y = 125.61 - 0.004x$
Fauna	September	female	2457.19	735.51	112.09	-0.008	$y = 112.09 - 0.008x$
Fauna	October	female	1938.20	34.79	91.88	-0.006	$y = 91.88 - 0.006x$
Fauna	November	female	353.00	24.84	101.35	-0.023	$y = 101.35 - 0.023x$
Fauna	December	female	436.49	621.88	87.78	0.002	$y = 87.78 + 0.002x$



**Table S3** Means and Standard deviations of the accumulation daily 95% kernel surface by month.

Month	Season	Mean	SD
January	NoBred	1902.977	720.057
February	Bred	1315.122	575.3051
March	Bred	1468.47	865.2336
April	Bred	2364.564	592.3092
May	Bred	2726.08	897.4024
June	Bred	2556.208	765.6784
July	NoBred	2624.407	889.5259
August	NoBred	1861.962	551.9305
September	NoBred	2186.027	749.7387
October	NoBred	2259.682	785.9645
November	NoBred	1592.318	957.9612
December	NoBred	1084.258	612.0869

**Table S4** Statistical ANOVA test of the accumulation daily 95% kernel surface by month and season.

ANOVA	Df	SumSq	MeanSq	Fvalue	Pr(>F)
Season	1	361163	361163	0.623	0.433
Month	10	17854366	1785437	3.078	0.003
Residuals	57	33068809	580155		

**Table S5** Statistical Tukey test of the accumulation daily 95% kernel surface comparing months.

Pair	diff	lwr	upr	p adj
August-April	355.2676	-1926.7183	1216.1831	0.9997
December-April	-1132.9713	-2774.298	508.3554	0.4540
February-April	-1049.4423	-2620.893	522.0083	0.5051
January-April	-314.2526	-1885.7033	1257.1981	0.9999
July-April	407.1774	-1164.2733	1978.6281	0.9991
June-April	191.64433	-1379.8063	1763.095	1.0000
March-April	-896.094	-2537.4207	745.2327	0.7777
May-April	361.516	-1209.9347	1932.9667	0.9997
November-April	-624.91094	-2196.3616	946.5397	0.9673
October-April	42.4524	-1528.9983	1613.9031	1.0000
September-April	-31.2026	-1602.6533	1540.2481	1.0000

Pair	diff	lwr	upr	p adj
December-August	-777.70367	-2349.1543	793.747	0.8669
February-August	-694.17473	-2192.4941	804.1447	0.9097
January-August	41.015	-1457.3044	1539.3344	1.0000
July-August	762.445	-735.87441	2260.7644	0.8449
June-August	546.91194	-951.40747	2045.2313	0.9827
March-August	-540.8264	-2112.2771	1030.6243	0.9891
May-August	716.7836	-781.53581	2215.103	0.8905
November-August	-269.64333	-1767.9627	1228.6761	1.0000
October-August	397.72	-1100.5994	1896.0394	0.9988
September-August	324.065	-1174.2544	1822.3844	0.9998
February-December	83.52894	-1487.9217	1654.9796	1.0000
January-December	818.71867	-752.73199	2390.1693	0.8242
July-December	1540.14867	-31.30199	3111.5993	0.0597
June-December	1324.6156	-246.83505	2896.0663	0.1790
March-December	236.87727	-1404.4494	1878.2039	1.0000
May-December	1494.48727	-76.96339	3065.9379	0.0767
November-December	508.06033	-1063.3903	2079.511	0.9934
October-December	1175.42367	-396.02699	2746.8743	0.3327
September-December	1101.76867	-469.68199	2673.2193	0.4300
January-February	735.18973	-763.12968	2233.5091	0.8732
July-February	1456.61973	-41.69968	2954.9391	0.0639
June-February	1241.08667	-257.23274	2739.4061	0.1985
March-February	153.34833	-1418.1023	1724.799	1.0000
May-February	1410.95833	-87.36108	2909.2777	0.0829
November-February	424.5314	-1073.788	1922.8508	0.9979
October-February	1091.89473	-406.42468	2590.2141	0.3711
September-February	1018.23973	-480.07968	2516.5591	0.4781
July-January	721.43	-776.88941	2219.7494	0.8863
June-January	505.89694	-992.42247	2004.2163	0.9906
March-January	-581.8414	-2153.2921	989.6093	0.9807
May-January	675.7686	-822.55081	2174.088	0.9236
November-January	-310.65833	-1808.9777	1187.6611	0.9999
October-January	356.705	-1141.6144	1855.0244	0.9996

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Pair	diff	lwr	upr	p adj
September-January	283.05	-1215.2694	1781.3694	1.0000
June-July	-215.53306	-1713.8525	1282.7863	1.0000
March-July	-1303.2714	-2874.7221	268.1793	0.1971
May-July	-45.6614	-1543.9808	1452.658	1.0000
November-July	-1032.0883	-2530.4077	466.2311	0.4572
October-July	-364.725	-1863.0444	1133.5944	0.9995
September-July	-438.38	-1936.6994	1059.9394	0.9972
March-June	-1087.7383	-2659.189	483.7123	0.4497
May-June	169.87167	-1328.4477	1668.1911	1.0000
November-June	-816.55527	-2314.8747	681.7641	0.7796
October-June	-149.19194	-1647.5114	1349.1275	1.0000
September-June	-222.84694	-1721.1664	1275.4725	1.0000
May-March	1257.61	-313.84066	2829.0607	0.2402
November-March	271.18306	-1300.2676	1842.6337	1.0000
October-March	938.5464	-632.90426	2509.9971	0.6685
September-March	864.8914	-706.55926	2436.3421	0.7689
November-May	-986.42694	-2484.7464	511.8925	0.5270
October-May	-319.0636	-1817.383	1179.2558	0.9999
September-May	-392.7186	-1891.038	1105.6008	0.9990
October-November	667.36333	-830.95608	2165.6827	0.9294
September-November	593.70833	-904.61108	2092.0277	0.9681
September-October	-73.655	-1571.9744	1424.6644	1.0000





## APÉNDICE III

Material suplementario del CAPÍTULO 3. Wildfire response of GPS-tracked Bonelli's eagles in eastern Spain.

### Materials and Methods

**Table S1** Summary information of 10 territorial Bonelli's eagles tracked by GPS/GSM telemetry in eastern Spain. Short-term period (Jun 01st – Aug 31st) and Long-term period 2015 – 2017. The untagging date of individuals that died are indicated with <sup>A</sup> and the individuals that its GPS stopped working are indicated with <sup>B</sup>. DWF: Distance to wildfire.

Individual	Code	Sex	Territory	DWF (km)	Tagging date	Untagging date	Analysis
Abel	M_ALF	M	Alfondeguilla	4.5	19/05/2015	16/09/2016 <sup>A</sup>	Short-term Long-term
Adan	M_ALF	M	Alfondeguilla	4.5	17/01/2017	-	Long-term
Aura	F_ALF	F	Alfondeguilla	4.5	19/05/2015	-	Short-term Long-term
Carbo	M_TAL	M	Tales	0	28/10/2015	-	Short-term Long-term
Carla	F_TAL	F	Tales	0	28/10/2015	20/04/2016 <sup>B</sup>	Long-term
				0	12/12/2016	2/012/2018 <sup>B</sup>	
Dino	M_SON	M	Soneja	8.6	29/10/2015	21/03/2018 <sup>A</sup>	Short-term Long-term
Dora	F_SON	F	Soneja	8.6	29/10/2015	21/03/2018 <sup>A</sup>	Short-term Long-term
Faig	M_AYO	M	Ayódar	6.8	08/06/2016	-	Short-term Long-term
Flora	F_AYO	F	Ayódar	6.8	08/06/2016	14/12/2016 <sup>A</sup>	Short-term Long-term
Fauna	F_AYO	F	Ayódar	6.8	17/05/2017	-	Long-term

**Table S2** Summary additional information of 10 territorial Bonelli's eagles' locations, tracked by GPS/GSM telemetry in eastern Spain during the Short-term period (01 Jun – Aug 31) and Long-term period (2015 – 2017).

Individual	Individual code	No. of GPS locations in Short-term analysis			Total locations	No. of GPS locations in Long-term analysis				Total locations
		Before	During	After		1	2	3	4	
Abel	M_ALF	9,852	1,491	5,332	16,675	63,077	6,875	-	-	182,589
Adan	M_ALF	9,574	1,492	5,303	16,369	-	-	53,294	59,343	
Aura	F_ALF	-	-	-	-	44,428	16,876	34,510	44,084	139,898
Carbo	M_TAL	9,918	1,499	5,364	16,781	33,441	14,954	45,558	44,425	138,378
Carla	F_TAL	-	-	-	-	14,754	1,683	50,949	37,563	104,949
Dino	M_SON	10,172	1,508	5,391	17,071	31,878	23,428	57,282	10,484	123,072
Dora	F_SON	10,173	1,509	5,398	17,08	42,779	24,210	57,299	10,449	134,737
Faig	M_AYO	8,060	1,439	5,344	14,843	8,059	23,835	55,002	54,426	141,322
Flora	F_AYO	7,932	1,473	5,064	14,469	7,932	18,701	-	-	100,506
Fauna	F_AYO	-	-	-	-	-	-	37,897	35,976	

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### Short-term differences in home range

**Table S3** Means, ( $\pm$ ) Standard Deviation (SD), Kruskal-Wallis and Wilcoxon results of the daily K95%, K50%, TDD and SLM of 7 individuals for the 3 short-term periods. Significant variables are highlighted in bold. ID: Individual.

ID	Variable	Mean $\pm$ SD			$\chi^2$	df	Wilcoxon test pair samples p-value			p-value
		Before	During	After			B-D	B-A	D-A	
M_ALF	K95% (km <sup>2</sup> )	34.43 $\pm$ 14.39	53.05 $\pm$ 13.49	37.37 $\pm$ 17.04	9.342	2	<b>0.006</b>	0.352	<b>0.039</b>	<b>0.009</b>
	K50% (km <sup>2</sup> )	8.62 $\pm$ 4.33	13.86 $\pm$ 6.01	9.59 $\pm$ 4.73	5.932	2	0.054	0.436	0.084	0.052
	TDD (km)	78.88 $\pm$ 21.63	87.57 $\pm$ 17.98	55.09 $\pm$ 21.47	22.379	2	0.289	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	SLM (m)	432.28 $\pm$ 113.97	470.36 $\pm$ 97.32	297.62 $\pm$ 110.92	23.798	2	0.419	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
F_ALF	K95% (km <sup>2</sup> )	36.67 $\pm$ 23.02	53.88 $\pm$ 11.27	34.99 $\pm$ 18.64	10.124	2	<b>0.004</b>	0.935	<b>0.007</b>	<b>0.006</b>
	K50% (km <sup>2</sup> )	8.62 $\pm$ 4.88	14.33 $\pm$ 4.86	8.62 $\pm$ 5.02	8.255	2	<b>0.011</b>	0.950	<b>0.020</b>	<b>0.016</b>
	TDD (km)	74.68 $\pm$ 22.83	79.33 $\pm$ 22.99	50.82 $\pm$ 18.53	21.411	2	0.607	<b>0.000</b>	<b>0.003</b>	<b>0.000</b>
	SLM (m)	421.71 $\pm$ 116.77	425.08 $\pm$ 120.94	274.68 $\pm$ 94.88	26.998	2	0.975	<b>0.000</b>	<b>0.003</b>	<b>0.000</b>
M_TAL	K95% (km <sup>2</sup> )	47.6 $\pm$ 27.5	76.6 $\pm$ 24.56	47.86 $\pm$ 24.58	8.182	2	<b>0.013</b>	0.943	<b>0.013</b>	<b>0.017</b>
	K50% (km <sup>2</sup> )	10.02 $\pm$ 5.84	15.47 $\pm$ 8.43	10.89 $\pm$ 6.97	3.51	2	0.190	0.710	0.190	0.173
	TDD (km)	80.69 $\pm$ 32.83	100.37 $\pm$ 26.53	83.84 $\pm$ 35.63	3.292	2	0.200	0.750	0.240	0.193
	SLM (m)	438.65 $\pm$ 171.76	535.47 $\pm$ 141.81	452.97 $\pm$ 190.3	3.027	2	0.230	0.840	0.250	0.220
M_SON	K95% (km <sup>2</sup> )	24.2 $\pm$ 11.44	38.83 $\pm$ 12.71	34.8 $\pm$ 14.47	15.034	2	<b>0.007</b>	<b>0.005</b>	0.373	<b>0.001</b>
	K50% (km <sup>2</sup> )	4.73 $\pm$ 3.12	9.85 $\pm$ 4.32	8.43 $\pm$ 4.18	21.938	2	<b>0.002</b>	<b>0.000</b>	0.435	<b>0.000</b>
	TDD (km)	61.85 $\pm$ 17.33	53.69 $\pm$ 13.59	46.48 $\pm$ 16.75	15.154	2	0.137	<b>0.001</b>	0.133	<b>0.001</b>
	SLM (m)	328.47 $\pm$ 92.33	287.1 $\pm$ 72.45	249.78 $\pm$ 87.47	14.518	2	0.207	<b>0.001</b>	0.207	<b>0.001</b>
F_SON	K95% (km <sup>2</sup> )	22.41 $\pm$ 12.99	39.95 $\pm$ 11.32	32.52 $\pm$ 16.23	14.407	2	<b>0.006</b>	<b>0.010</b>	0.118	<b>0.001</b>
	K50% (km <sup>2</sup> )	4.33 $\pm$ 3.35	9.51 $\pm$ 3.96	7.61 $\pm$ 4.34	20.365	2	<b>0.001</b>	<b>0.001</b>	0.266	<b>0.000</b>
	TDD (km)	55.56 $\pm$ 18.99	57.32 $\pm$ 15.2	43.15 $\pm$ 18.79	9.792	2	0.793	<b>0.011</b>	<b>0.043</b>	<b>0.007</b>
	SLM (m)	294.86 $\pm$ 100.58	304.17 $\pm$ 81.38	231.46 $\pm$ 98.63	9.173	2	0.777	<b>0.014</b>	0.053	<b>0.010</b>
M_AYO	K95% (km <sup>2</sup> )	29.58 $\pm$ 15.31	30.06 $\pm$ 11.99	23.91 $\pm$ 14.5	2.763	2	0.880	0.310	0.310	0.251
	K50% (km <sup>2</sup> )	8.23 $\pm$ 4.79	8.96 $\pm$ 3.11	6.59 $\pm$ 4.31	3.829	2	0.500	0.210	0.200	0.147
	TDD (km)	47.55 $\pm$ 19.45	47.28 $\pm$ 14.98	40.43 $\pm$ 15.03	2.856	2	0.950	0.300	0.560	0.240
	SLM (m)	273.58 $\pm$ 103.24	261.19 $\pm$ 76.56	219.37 $\pm$ 80.1	5.049	2	0.879	0.086	0.332	0.080
F_AYO	K95% (km <sup>2</sup> )	32.39 $\pm$ 18.24	30.48 $\pm$ 12.8	25.98 $\pm$ 14.48	1.391	2	0.880	0.710	0.880	0.499
	K50% (km <sup>2</sup> )	8.64 $\pm$ 5.39	8.93 $\pm$ 3.31	6.95 $\pm$ 4.28	1.577	2	0.650	0.500	0.500	0.455
	TDD (km)	51.79 $\pm$ 21.4	50.58 $\pm$ 13.39	49.37 $\pm$ 17.84	0.217	2	0.920	0.920	0.920	0.897
	SLM (m)	303.56 $\pm$ 112.17	276.01 $\pm$ 78.92	290.49 $\pm$ 99.47	0.577	2	0.870	0.870	0.870	0.749



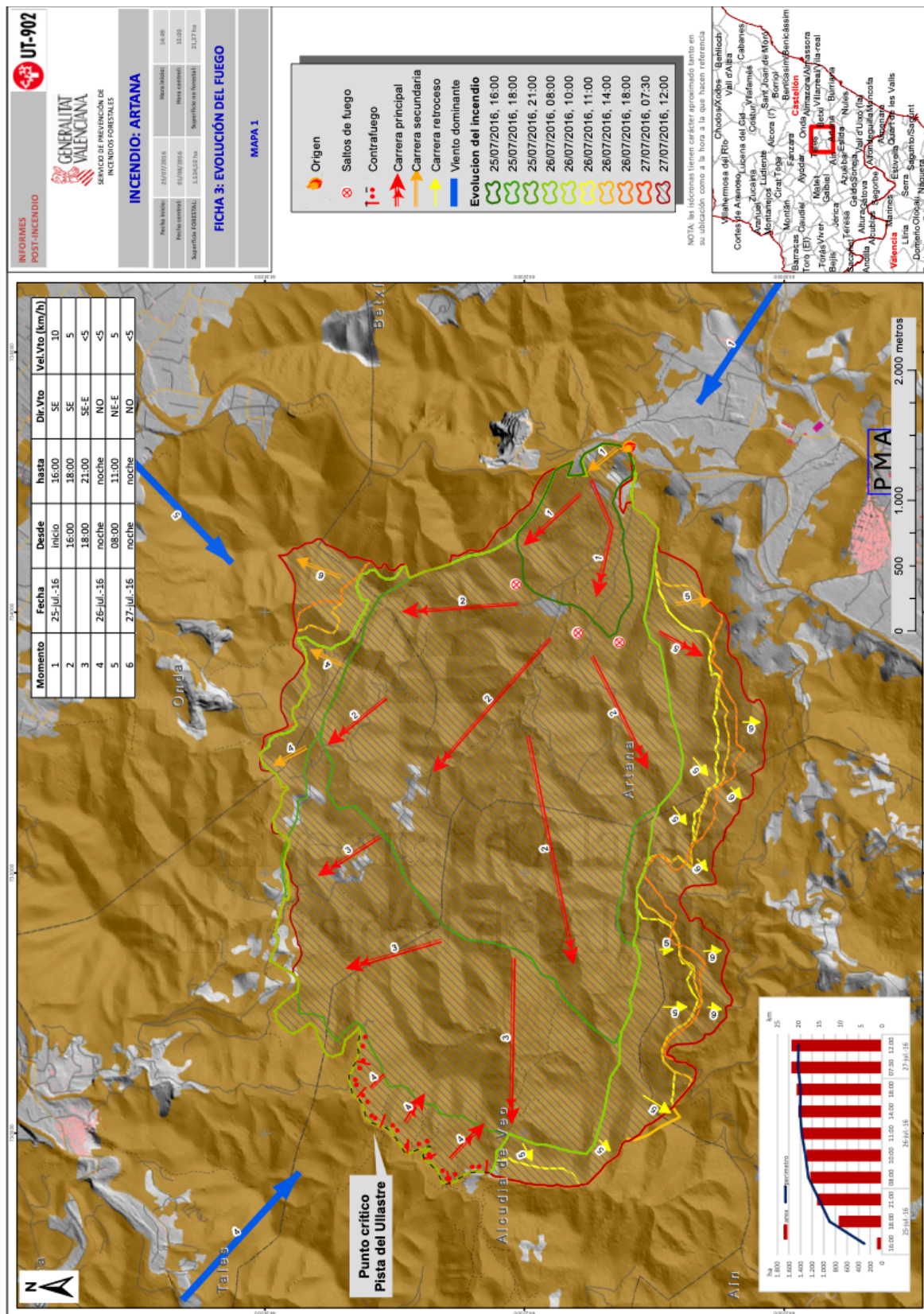
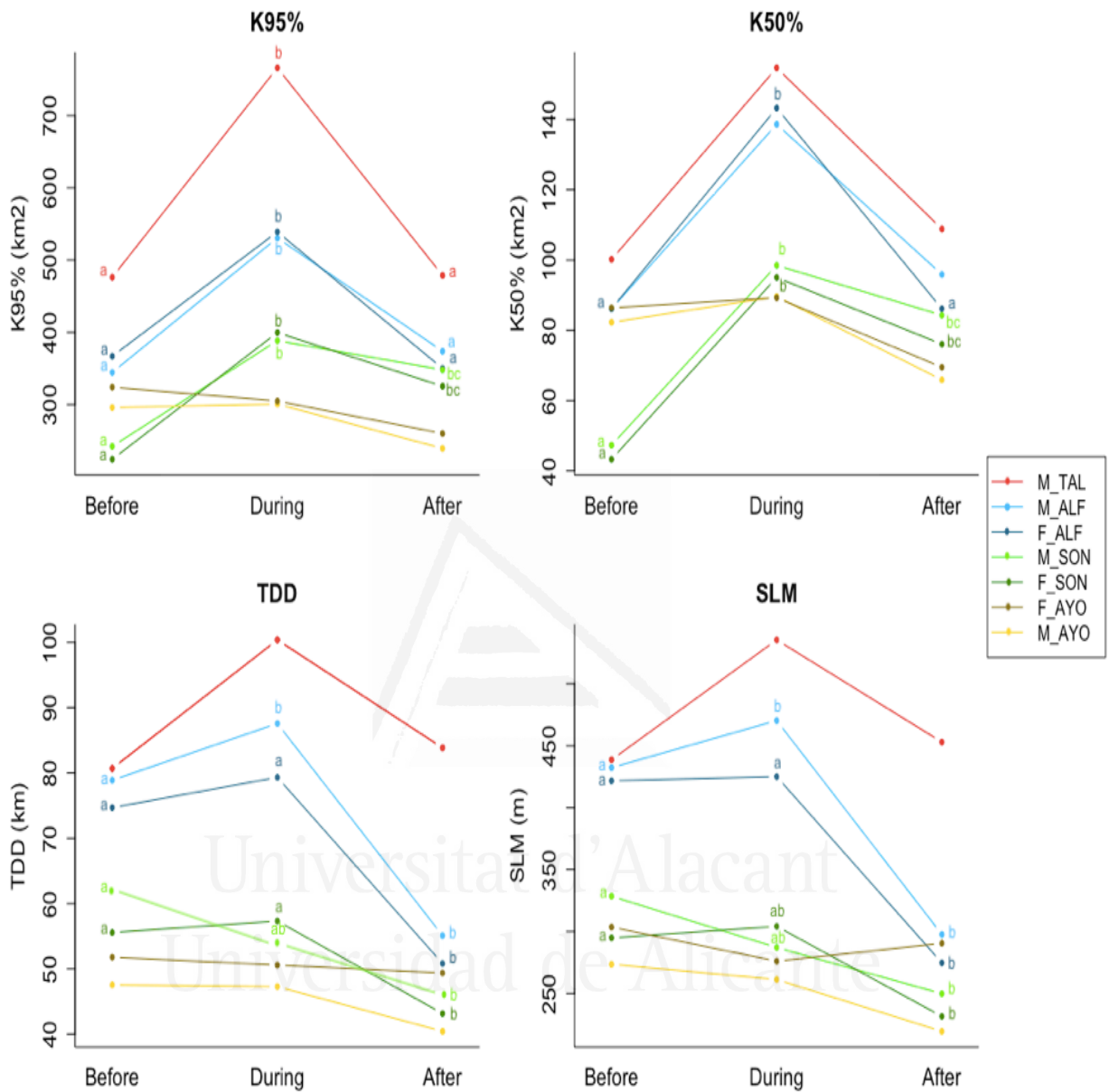
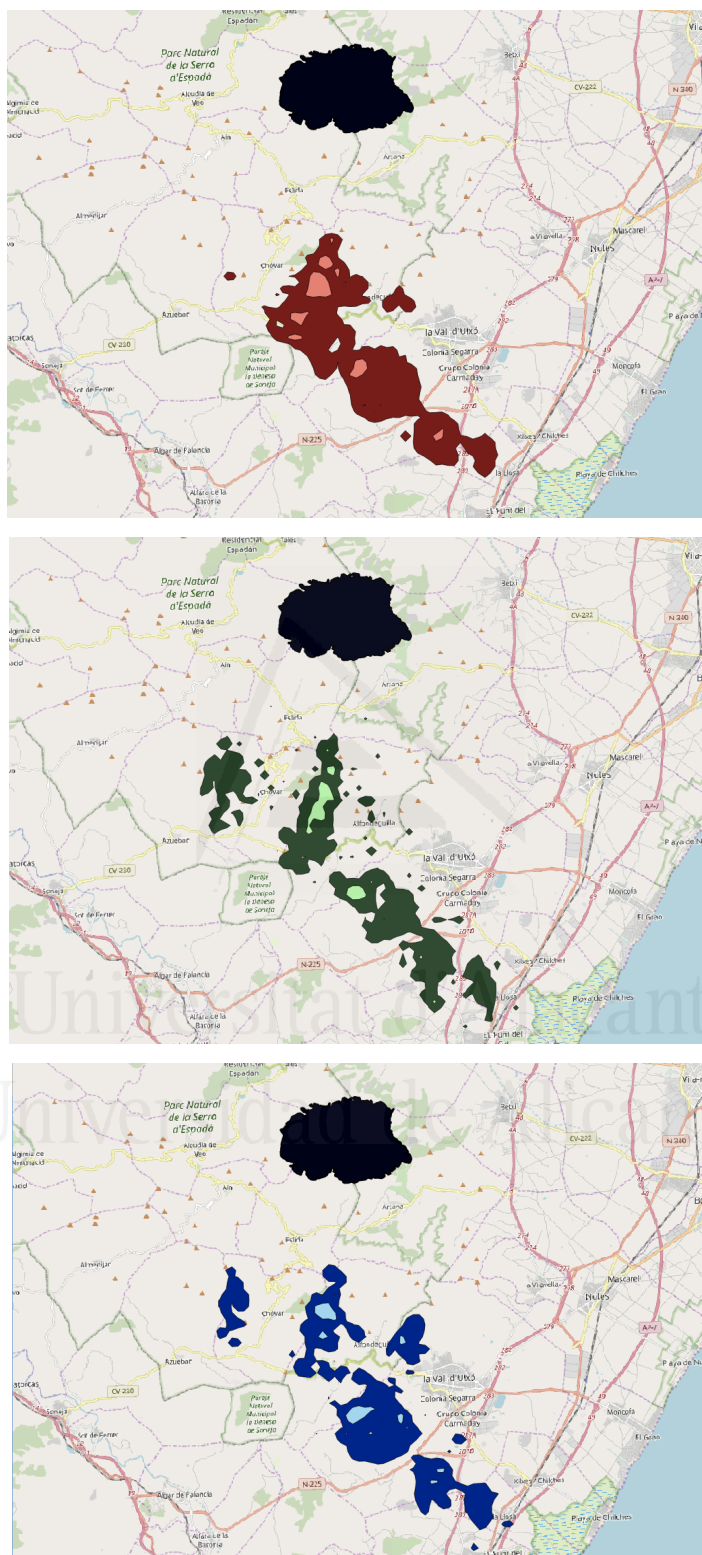


Figure S1 Detailed map of the evolution of the forest fire (progress steps, day and time of advance, wind direction, number of hectares burned, etc.).

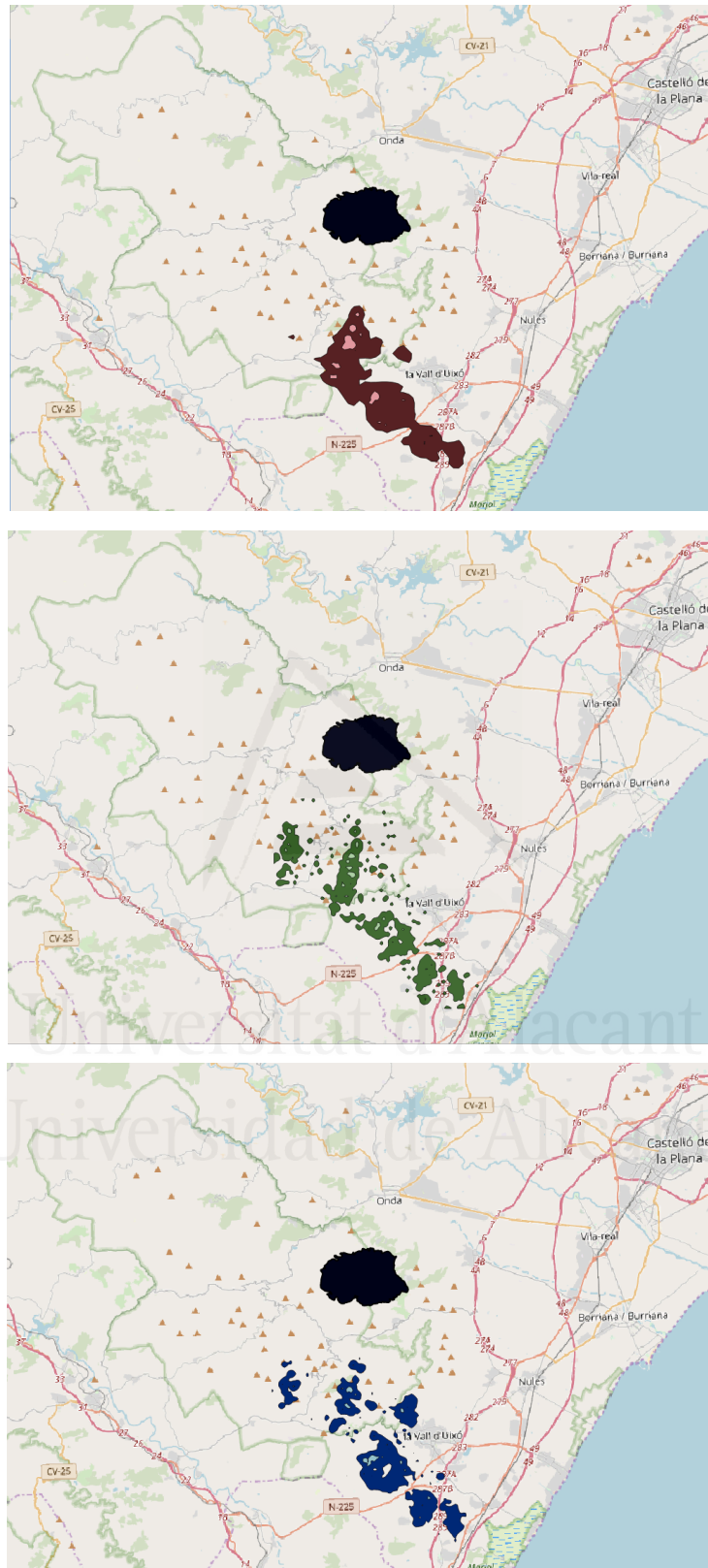


**Figure S2** Short-term differences in the spatial parameters before, during, and after the wildfire of seven Bonelli's eagles (three pairs and the male directly affected by the fire (M\_TAL)). Abbreviations: K95% = 95% kernel; K50% = 50% kernel; TDD = total daily distance; SLM = step length mean. The significance between periods (before, during, after) is shown with letters; lines with no letters refers to non-significant changes among the three periods.

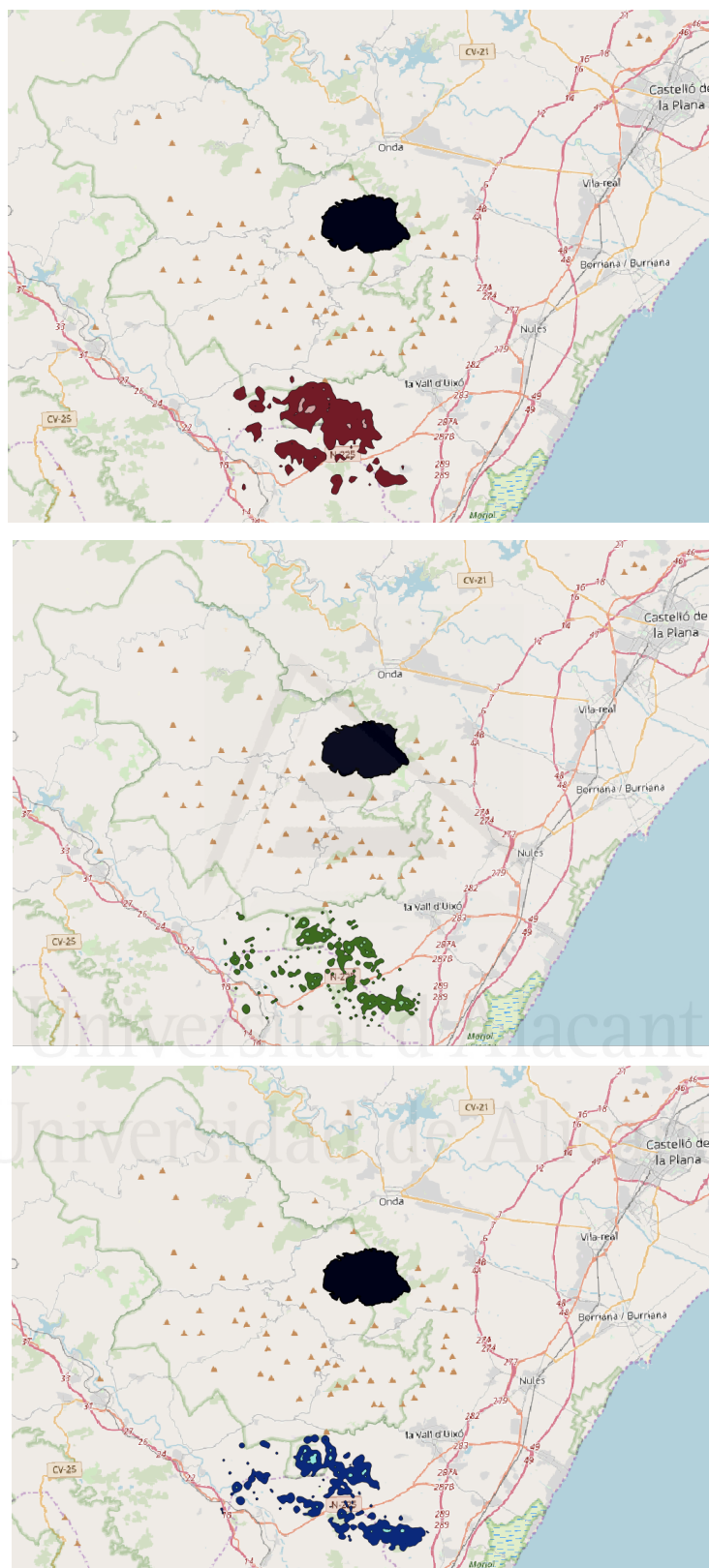
**K95% and K50% maps territories of the 7 Bonelli's eagles**



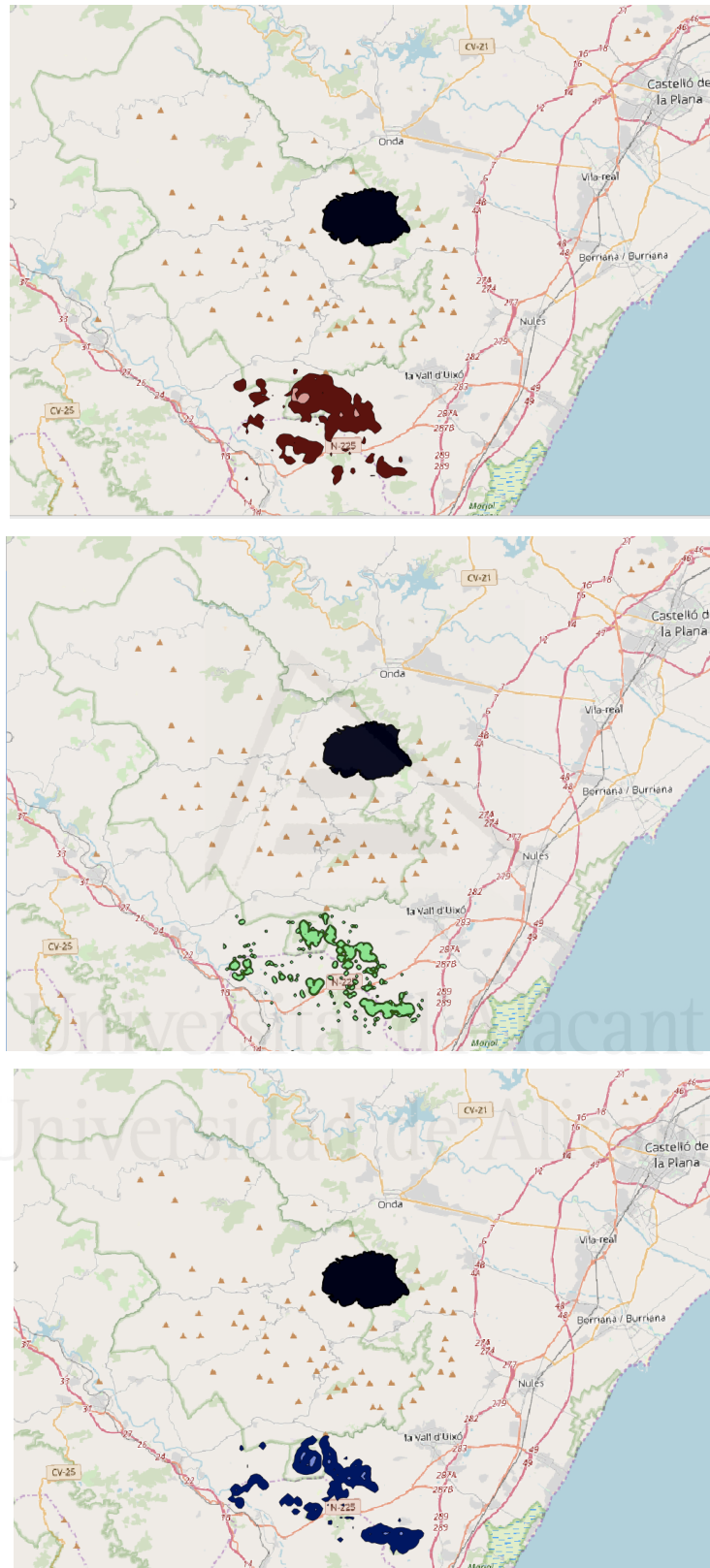
**Figure S3** K50% and K95% of M\_ALF before the wildfire (red 01/06/16 - 24/07/16), during the wildfire (Green; 25/07/16 - 01/08/16) and after the wildfire (blue; 02/08/16 - 31/08/16).



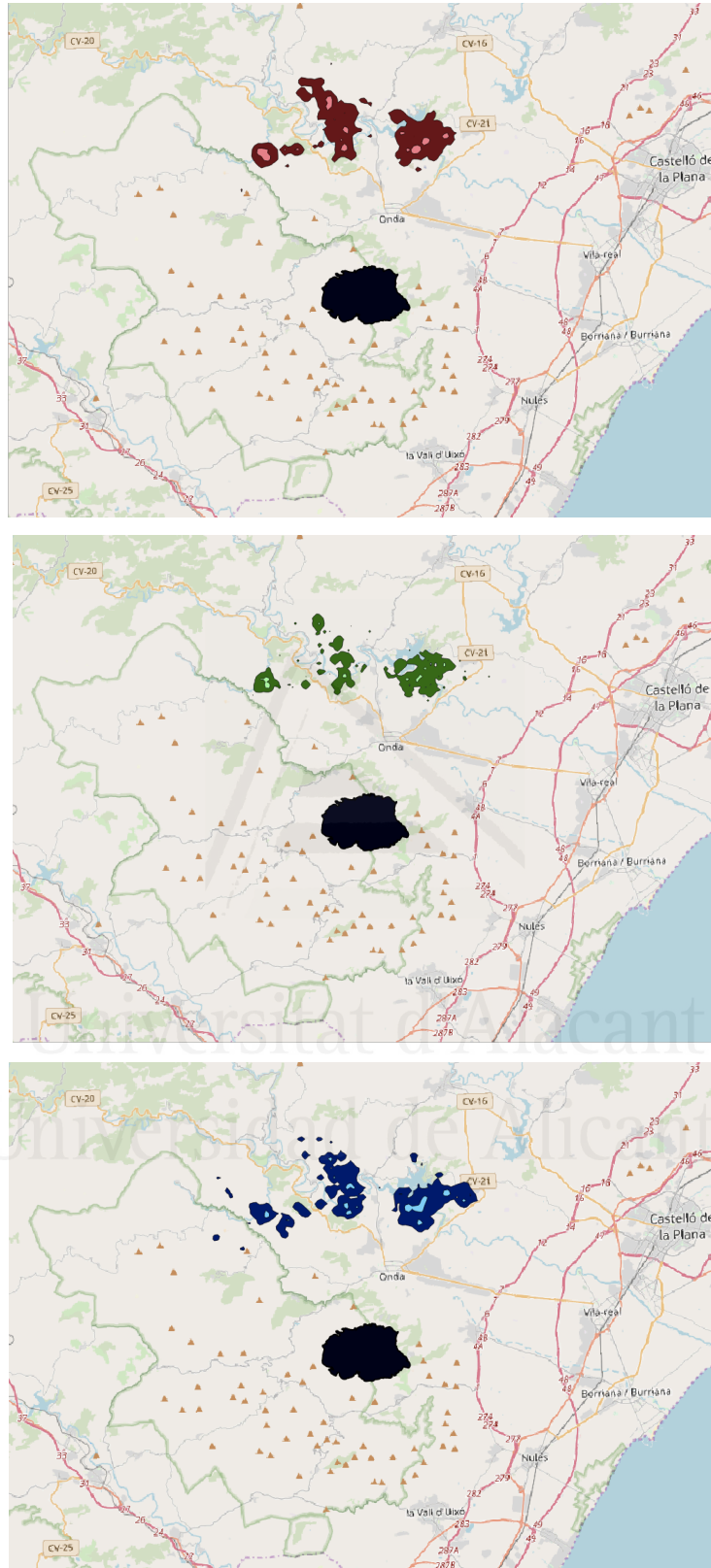
**Figure S4** K50% and K95% of F\_ALF before the wildfire (red; 01/06/16 - 24/07/16), during the wildfire (Green; 25/07/16 - 01/08/16) and after the wildfire (blue; 02/08/16 - 31/08/16).



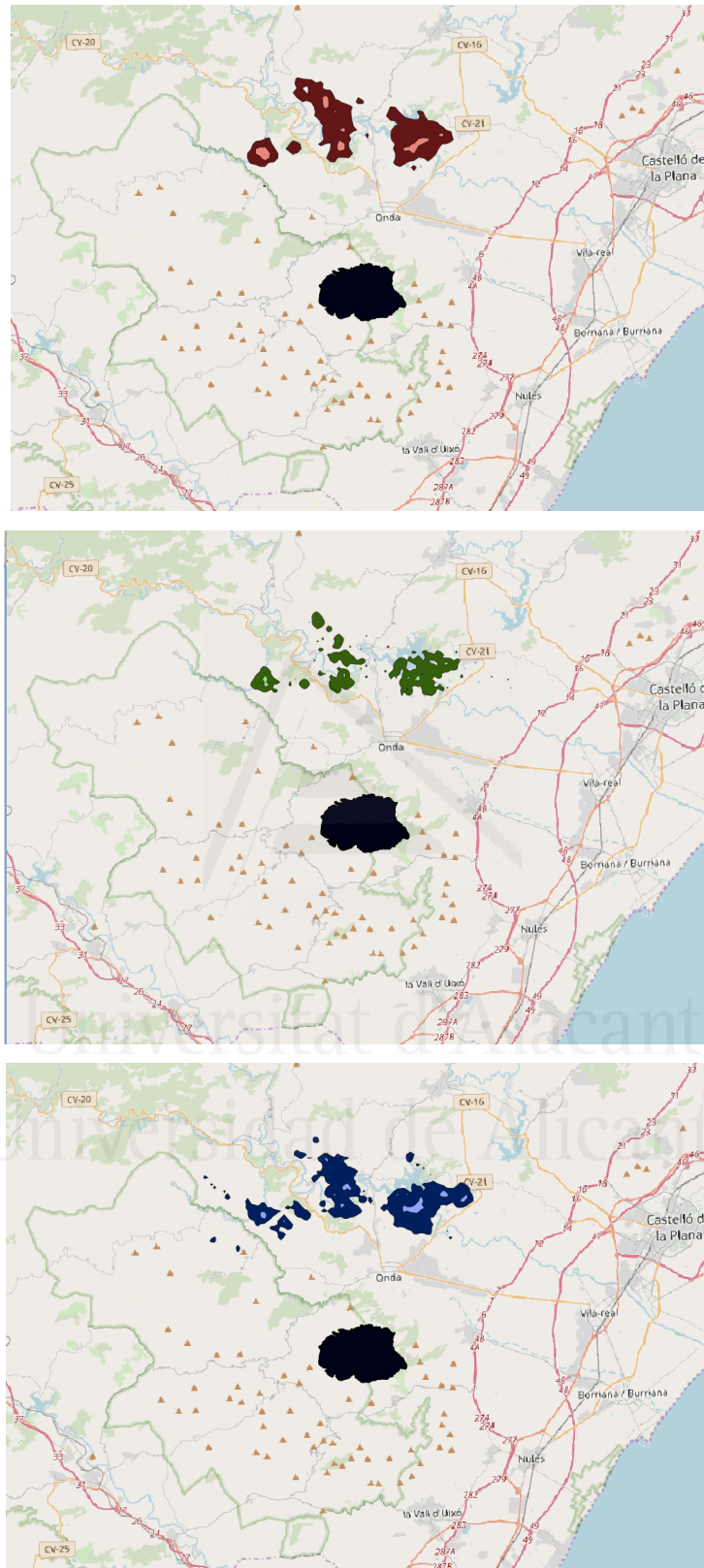
**Figure S5** K50% and K95% of  $M_{SON}$  before the wildfire (red; 01/06/16 - 24/07/16), during the wildfire (Green; 25/07/16 - 01/08/16) and after the wildfire (blue; 02/08/16 - 31/08/16).



**Figure S6** K50% and K95% of F\_SON before the wildfire (red; 01/06/16 - 24/07/16), during the wildfire (Green; 25/07/16 - 01/08/16) and after the wildfire (blue; 02/08/16 - 31/08/16).



**Figure S7** K50% and K95% of M\_AYO before the wildfire (red; 01/06/16 - 24/07/16), during the wildfire (Green; 25/07/16 - 01/08/16) and after the wildfire (blue; 02/08/16 - 31/08/16).



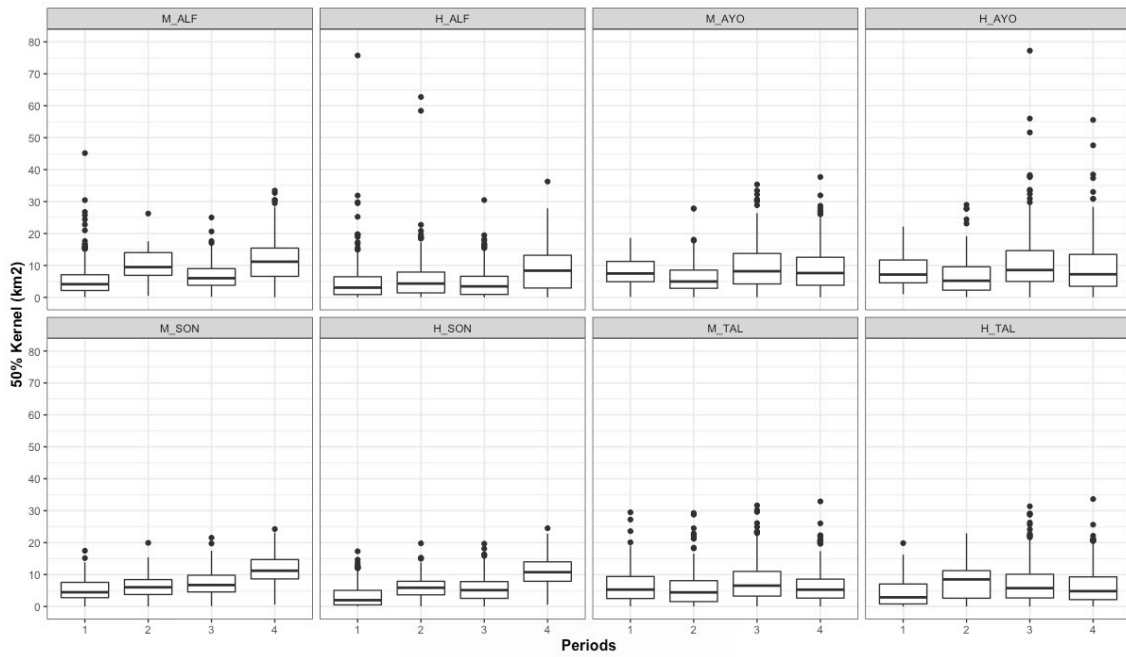
**Figure S8** K50% and K95% of F\_AYO before the wildfire (red; 01/06/16 - 24/07/16), during the wildfire (Green; 25/07/16 - 01/08/16) and after the wildfire (blue; 02/08/16 - 31/08/16).



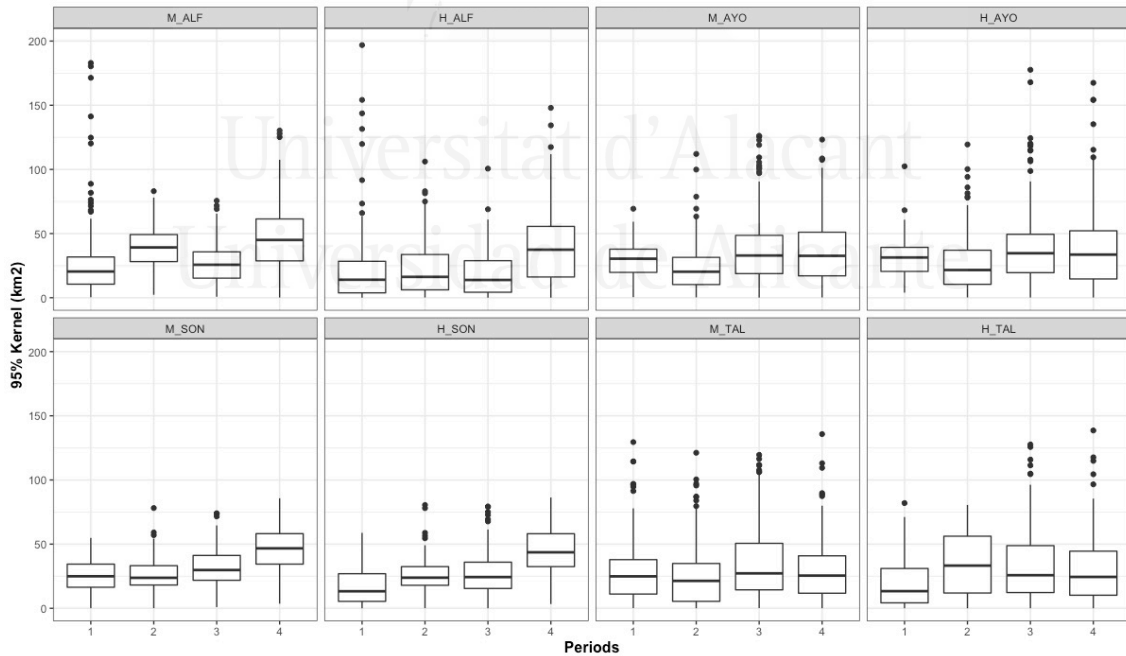
### Long-term differences in the home range

**Table S4** Statistical results of the Kruskal-Wallis analysis between the four periods selected for the 4 variables. In addition, the statistical results of the Wilcoxon test in pairs are shown. Significant results are shown in bold with a value of  $p < 0.05$ . 1: 2015-2016 period before the wildfire; 2: 2016 period after the wildfire; 3: 2017 period; 4: 2018 period.

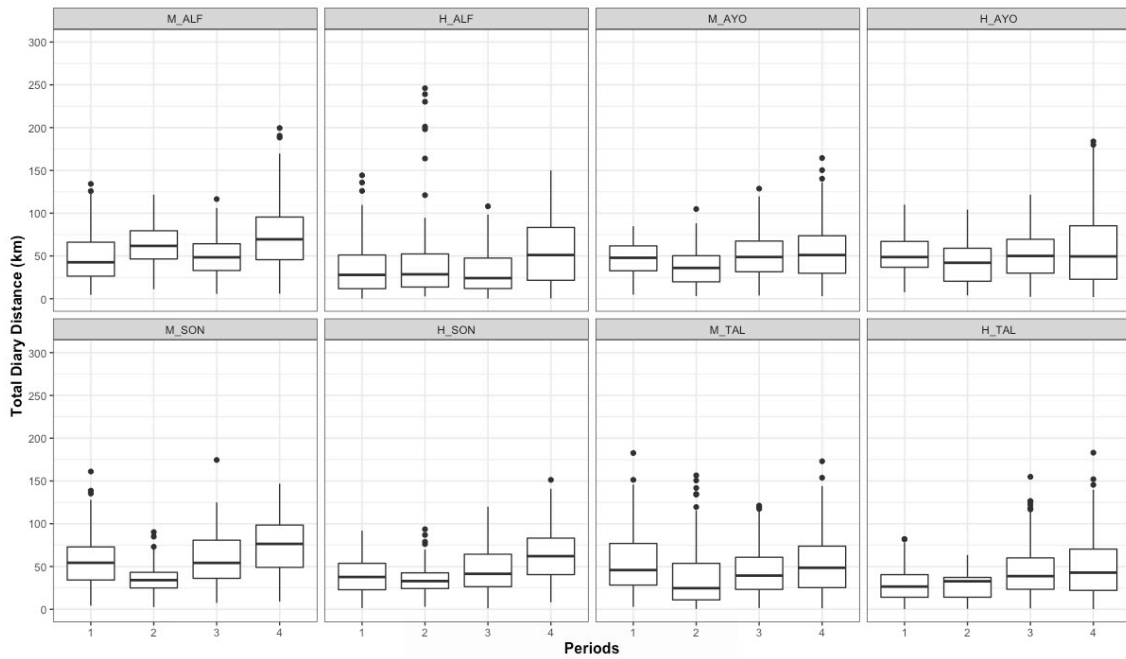
ID	Variable	$\chi^2$	df	Wilcoxon test pair samples p-Value						P
				1:2	1:3	1:4	2:3	2:4	3:4	
M_ALF	K50%	247.86	3	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.360	<b>0.000</b>	<b>0.000</b>
	K95%	244.16	3	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.160	<b>0.000</b>	<b>0.000</b>
	TDD	123.3	3	<b>0.004</b>	<b>0.049</b>	<b>0.000</b>	0.089	0.086	<b>0.000</b>	<b>0.000</b>
	SLM	87371	3	0.654	0.337	<b>0.000</b>	0.337	<b>0.003</b>	<b>0.000</b>	<b>0.000</b>
H_ALF	K50%	124.54	3	<b>0.000</b>	0.604	<b>0.000</b>	<b>0.001</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	K95%	154.23	3	<b>0.004</b>	0.883	<b>0.000</b>	<b>0.004</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	TDD	94338	3	0.570	0.160	<b>0.000</b>	0.140	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	SLM	55878	3	<b>0.027</b>	0.280	<b>0.000</b>	0.189	<b>0.007</b>	<b>0.000</b>	<b>0.000</b>
M_TAL	K50%	20151	3	0.113	<b>0.007</b>	0.864	<b>0.001</b>	0.071	<b>0.007</b>	<b>0.000</b>
	K95%	17387	3	<b>0.039</b>	<b>0.039</b>	0.572	<b>0.001</b>	<b>0.022</b>	0.053	<b>0.001</b>
	TDD	43579	3	<b>0.000</b>	<b>0.003</b>	0.506	<b>0.000</b>	<b>0.000</b>	<b>0.006</b>	<b>0.000</b>
	SLM	16739	3	0.712	<b>0.003</b>	0.770	0.152	0.642	<b>0.001</b>	<b>0.001</b>
H_TAL	K50%	30722	3	<b>0.031</b>	<b>0.000</b>	<b>0.001</b>	0.538	0.289	0.065	<b>0.000</b>
	K95%	28309	3	<b>0.037</b>	<b>0.000</b>	<b>0.000</b>	0.615	0.497	0.347	<b>0.000</b>
	TDD	40623	3	0.860	<b>0.000</b>	<b>0.000</b>	<b>0.026</b>	<b>0.016</b>	0.159	<b>0.000</b>
	SLM	23571	3	0.759	0.412	<b>0.000</b>	0.926	0.412	<b>0.000</b>	<b>0.000</b>
M_SON	K50%	117.95	3	<b>0.002</b>	<b>0.000</b>	<b>0.000</b>	<b>0.006</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	K95%	96404	3	0.730	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	TDD	112.09	3	<b>0.000</b>	0.364	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	SLM	120.08	3	<b>0.000</b>	0.140	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
H_SON	K50%	176.06	3	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.038</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	K95%	133.7	3	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.960	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	TDD	62334	3	<b>0.002</b>	<b>0.012</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	SLM	100.1	3	0.141	<b>0.002</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
M_AYO	K50%	32505	3	<b>0.005</b>	0.502	0.885	<b>0.000</b>	<b>0.000</b>	0.100	<b>0.000</b>
	K95%	43231	3	<b>0.010</b>	0.208	0.250	<b>0.000</b>	<b>0.000</b>	0.684	<b>0.000</b>
	TDD	42442	3	<b>0.003</b>	0.590	0.431	<b>0.000</b>	<b>0.000</b>	0.431	<b>0.000</b>
	SLM	53041	3	0.118	<b>0.015</b>	0.096	<b>0.000</b>	<b>0.000</b>	0.313	<b>0.000</b>
H_AYO	K50%	24.86	3	<b>0.025</b>	0.231	0.847	<b>0.000</b>	<b>0.006</b>	<b>0.025</b>	<b>0.000</b>
	K95%	27953	3	<b>0.020</b>	0.166	0.472	<b>0.000</b>	<b>0.000</b>	0.206	<b>0.000</b>
	TDD	14441	3	<b>0.016</b>	0.990	0.990	<b>0.002</b>	<b>0.005</b>	0.990	<b>0.002</b>
	SLM	119.58	3	0.297	<b>0.002</b>	<b>0.000</b>	<b>0.004</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>



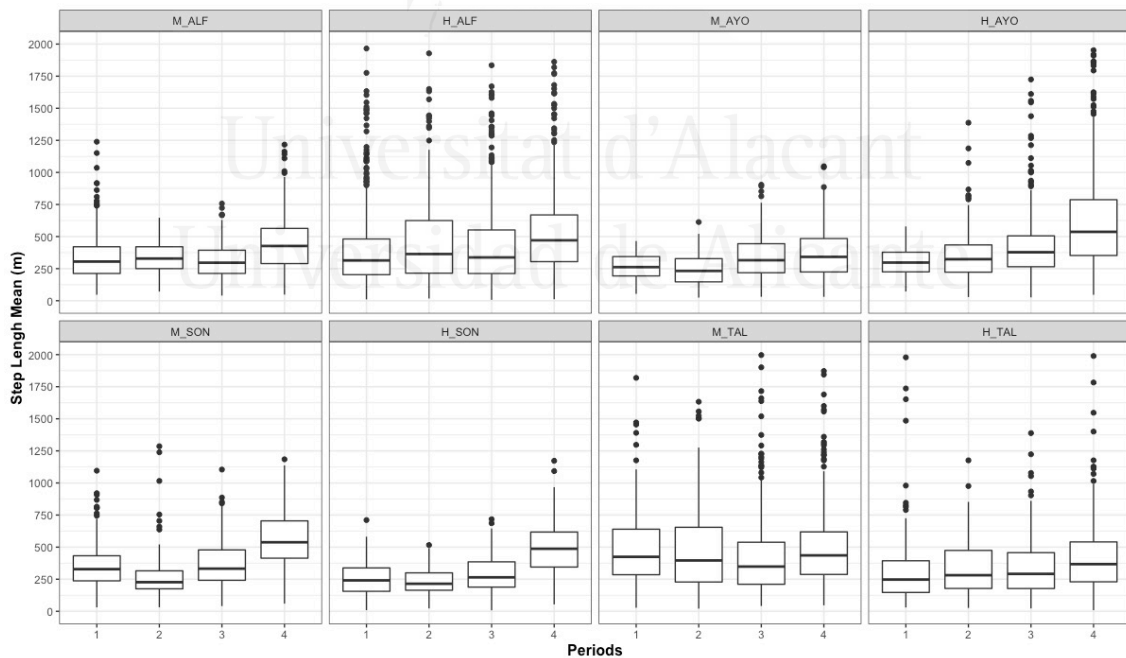
**Figure S9** Boxplot showing the differences of K<sub>50%</sub> (km<sup>2</sup>), of the 7 Bonelli's eagles in the 4 different periods (1: 2015-2016 period before the wildfire; 2: 2016 period after the wildfire; 3: 2017 period; 4: 2018 period).



**Figure S10** Boxplot showing the differences of K<sub>95%</sub> (km<sup>2</sup>), of the 7 Bonelli's eagles in the 4 different periods (1: 2015-2016 period before the wildfire; 2: 2016 period after the wildfire; 3: 2017 period; 4: 2018 period).



**Figure S11** Boxplot showing the differences of TDD (km), of the 7 Bonelli's eagles in the 4 different periods (1: 2015-2016 period before the wildfire; 2: 2016 period after the wildfire; 3: 2017 period; 4: 2018 period).



**Figure S12** Boxplot showing the differences of SLM (m) of the 7 Bonelli's eagles in the 4 different periods (1: 2015-2016 period before the wildfire; 2: 2016 period after the wildfire; 3: 2017 period; 4: 2018 period).





## APÉNDICE IV

Material suplementario del CAPÍTULO 4. A new view of territoriality. Design of protected areas with its application.

**Table S1** Summary information of 51 Bonelli's eagles monitored by GPS/GSM telemetry in eastern Spain (period: 2015 – 2021)

Individual	Territory	Sex	Tagging date	End day of data transmission
Abel	A	Male	19/05/2015	02/09/2016
Adan	A	Male	31/01/2017	16/06/2020
Aura	A	Female	19/05/2015	21/05/2021
Berta	B	Female	10/06/2015	04/07/2015
Blas	B	Male	10/06/2015	27/06/2016
Boira	B	Female	06/11/2015	28/06/2016
Boj	B	Male	11/04/2017	19/06/2017
Bruma	B	Female	11/04/2017	21/05/2021
Carbo	C	Male	28/10/2015	25/03/2020
Carla	C	Female	28/10/2015	30/11/2018
Dino	D	Male	29/10/2015	21/03/2018
Dora	D	Female	29/10/2015	21/03/2018
Enebro	E	Male	06/06/2016	06/07/2020
Faig	F	Male	08/06/2016	21/05/2021
Fauna	F	Female	18/05/2017	21/05/2021
Flora	F	Female	08/06/2016	14/12/2016
Garra	G	Female	07/10/2016	24/02/2019
Gel	G	Male	07/10/2016	21/05/2021
Haeckel	H	Male	20/04/2017	01/04/2018
Helios	H	Male	06/10/2016	26/01/2017
Hydra	H	Female	06/10/2016	07/03/2018
Iris	I	Female	09/12/2016	27/03/2017
Isis	I	Male	09/12/2016	20/01/2017
Jara	J	Female	14/06/2017	21/05/2021
Juan	J	Male	05/06/2017	13/11/2020

Individual	Territory	Sex	Tagging date	End day of data transmission
Karma	K	Female	06/06/2017	29/03/2018
Koko	K	Male	13/09/2017	29/03/2018
Linneo	L	Male	11/07/2017	21/05/2021
Lucy	L	Female	11/07/2017	31/12/2019
Margulis	M	Female	06/06/2018	21/05/2021
Mendel	M	Male	06/06/2018	21/05/2021
Newton	N	Male	07/06/2018	31/03/2019
Nube	O	Female	06/06/2018	31/12/2018
Ochoa	O	Male	08/06/2018	21/05/2021
Olympia	O	Female	11/06/2018	21/05/2021
Pino	P	Male	23/06/2020	06/07/2020
Pluma	P	Female	28/01/2019	21/05/2021
Popper	P	Male	28/01/2019	16/10/2019
Rosalind	R	Female	03/06/2019	21/05/2021
Rutherford	R	Male	03/06/2019	21/05/2021
Sabina	S	Female	13/06/2019	21/02/2020
Salvia	S	Female	09/06/2020	21/05/2021
Sauce	S	Male	12/06/2019	21/05/2021
Taiga	T	Female	21/06/2019	21/05/2021
Tejo	T	Male	15/06/2019	21/05/2021
Ulex	U	Male	08/10/2019	31/12/2020
Uva	U	Female	08/10/2019	01/01/2021
Vera	V	Female	07/11/2019	21/05/2021
Verdi	V	Male	07/11/2019	21/05/2021
VillenaFemale	W	Female	17/05/2018	31/12/2019
VillenaMale	W	Male	17/05/2018	21/05/2021

**Table S2** Generalized Linear Mixed Model (GLMMs) results of variation in K95%, K75%, K50% and territory eccentricity taking into account the ID, the SEX and the YEAR within each territory. Significant values are highlighted in bold.

Value	Variable	Estimate	Std. Error	t val.	d.f.	p-Value
K95%	(Intercept)	147.995	100.72	1.469	103	0.145
	IDAdan	8.638	36.022	0.24	103	0.811
	IDAura	-91.884	56.722	-1.62	103	0.108
	IDBerta	-91.139	137.268	-0.664	103	0.508
	IDBlas	1.029	126.016	0.008	103	0.994
	IDBoira	-99.342	134.19	-0.74	103	0.461
	IDBoj	-21.566	129.728	-0.166	103	0.868
	IDBruma	-109.732	133.272	-0.823	103	0.412
	IDCarbo	40.092	124.282	0.323	103	0.748
	IDCarla	-55.341	132.829	-0.417	103	0.678
	IDDino	-3.827	124.665	-0.031	103	0.976
	IDDora	-103.559	132.829	-0.78	103	0.437
	IDEnebro	50.146	124.674	0.402	103	0.688
	IDFaig	13.434	124.508	0.108	103	0.914
	IDFauna	-72.804	133.272	-0.546	103	0.586
	IDFlora	-74.996	137.291	-0.546	103	0.586
	IDGarra	-91.537	133.176	-0.687	103	0.493
	IDGel	10.343	124.508	0.083	103	0.934
	IDHaeckel	-10.882	126.655	-0.086	103	0.932
	IDHelios	-18.127	126.365	-0.143	103	0.886
	IDHydra	-120.771	133.493	-0.905	103	0.368
	IDIris	-95.814	134.534	-0.712	103	0.478
	IDIsis	-7.912	126.365	-0.063	103	0.950
	IDJara	-115.884	133.272	-0.87	103	0.387
	IDJuan	-4.088	125.146	-0.033	103	0.974
	IDKarma	-78.815	134.607	-0.586	103	0.559
	IDKoko	21.947	126.655	0.173	103	0.863
	IDLinneo	64.302	124.86	0.515	103	0.608
	IDLucy	-29.297	133.83	-0.219	103	0.827



Value	Variable	Estimate	Std. Error	t val.	d.f.	p-Value
	IDMargulis	-89.102	133.653	-0.667	103	0.506
	IDMendel	11.07	125.227	0.088	103	0.930
	IDNewton	96.046	126.728	0.758	103	0.450
	IDNube	-4.591	137.332	-0.033	103	0.973
	IDOchoa	49.866	125.227	0.398	103	0.691
	IDOlympia	-36.838	133.653	-0.276	103	0.783
	IDPino	18.746	129.901	0.144	103	0.886
	IDPluma	-109.313	134.396	-0.813	103	0.418
	IDPopper	-0.619	129.857	-0.005	103	0.996
	IDRosalind	-125.516	134.396	-0.934	103	0.353
	IDRutherford	-29.381	125.811	-0.234	103	0.816
	IDSabina	-75.33	135.315	-0.557	103	0.579
	IDSalvia	-40.713	135.422	-0.301	103	0.764
	IDSauce	57.058	125.811	0.454	103	0.651
	IDTaiga	-112.807	134.396	-0.839	103	0.403
	IDTejo	-19.651	125.811	-0.156	103	0.876
	IDUlex	234.306	125.811	1.862	103	0.065
	IDUva	36.86	135.315	0.272	103	0.786
	IDVera	-110.589	134.396	-0.823	103	0.412
	IDVerdi	-6.843	125.811	-0.054	103	0.957
	IDVillenaFemale	-85.36	134.836	-0.633	103	0.528
	IDVillenaMale	17.603	125.811	0.14	103	0.889
	<b>SEXMale</b>	<b>-96.934</b>	<b>46.118</b>	<b>-2.102</b>	<b>103</b>	<b>0.038</b>
	YEAR2016	-1.363	17.974	-0.076	103	0.940
	YEAR2017	9.733	18.771	0.519	103	0.605
	YEAR2018	10.458	18.846	0.555	103	0.580
	YEAR2019	8.909	19.594	0.455	103	0.650
	YEAR2020	7.279	19.869	0.366	103	0.715
	YEAR2021	19.924	20.533	0.97	103	0.334
K75%	<b>(Intercept)</b>	<b>4.337</b>	<b>0.631</b>	<b>6.872</b>	<b>103</b>	<b>0.000</b>
	IDAdan	0.337	0.308	1.092	103	0.277
	IDAura	-1.248	0.485	-2.571	103	0.012

Value	Variable	Estimate	Std. Error	t val.	d.f.	p-Value
	IDBerta	-1.294	0.831	-1.557	103	0.123
	IDBlas	-0.182	0.688	-0.265	103	0.792
	IDBoira	-1.789	0.793	-2.255	103	0.026
	IDBoj	-0.218	0.737	-0.296	103	0.768
	<b>IDBruma</b>	<b>-1.693</b>	<b>0.782</b>	<b>-2.165</b>	<b>103</b>	<b>0.033</b>
	IDCarbo	0.652	0.665	0.981	103	0.329
	IDCarla	-0.771	0.776	-0.993	103	0.323
	IDDino	0.129	0.67	0.192	103	0.848
	IDDora	-1.499	0.776	-1.93	103	0.056
	IDEnebro	0.8	0.67	1.193	103	0.236
	IDFaig	0.508	0.668	0.761	103	0.448
	IDFauna	-0.775	0.782	-0.991	103	0.324
	IDFlora	-0.835	0.831	-1.004	103	0.318
	IDGarra	-1.359	0.781	-1.74	103	0.085
	IDGel	0.275	0.668	0.412	103	0.681
	IDHaeckel	-0.175	0.697	-0.251	103	0.802
	IDHelios	-0.116	0.693	-0.168	103	0.867
	<b>IDHydra</b>	<b>-2.023</b>	<b>0.785</b>	<b>-2.579</b>	<b>103</b>	<b>0.011</b>
	IDIris	-1.383	0.798	-1.734	103	0.086
	IDIsis	0.034	0.693	0.049	103	0.961
	<b>IDJara</b>	<b>-1.8</b>	<b>0.782</b>	<b>-2.303</b>	<b>103</b>	<b>0.023</b>
	IDJuan	-0.089	0.677	-0.131	103	0.896
	IDKarma	-1.158	0.798	-1.45	103	0.150
	IDKoko	0.462	0.697	0.663	103	0.509
	IDLinneo	0.941	0.673	1.399	103	0.165
	IDLucy	-0.479	0.789	-0.608	103	0.545
	IDMargulis	-1.08	0.787	-1.373	103	0.173
	IDMendel	0.477	0.678	0.705	103	0.483
	IDNewton	1.057	0.698	1.515	103	0.133
	IDNube	-0.55	0.832	-0.661	103	0.510
	IDOchoa	0.47	0.678	0.694	103	0.489
	IDOlympia	-1.029	0.787	-1.307	103	0.194

Value	Variable	Estimate	Std. Error	t val.	d.f.	p-Value
	IDPino	0.802	0.739	1.086	103	0.280
	IDPluma	-1.259	0.796	-1.582	103	0.117
	IDPopper	0.413	0.739	0.559	103	0.577
	<b>IDRosalind</b>	<b>-1.656</b>	<b>0.796</b>	<b>-2.081</b>	<b>103</b>	<b>0.040</b>
	IDRutherford	-0.22	0.685	-0.321	103	0.749
	IDSabina	-1.253	0.807	-1.552	103	0.124
	IDSalvia	-0.436	0.809	-0.539	103	0.591
	IDSauce	1.061	0.685	1.548	103	0.125
	IDTaiga	-1.573	0.796	-1.977	103	0.051
	IDTejo	-0.11	0.685	-0.16	103	0.873
	<b>IDUlex</b>	<b>1.369</b>	<b>0.685</b>	<b>1.997</b>	<b>103</b>	<b>0.048</b>
	IDUva	-0.493	0.807	-0.611	103	0.542
	IDVera	-1.419	0.796	-1.783	103	0.077
	IDVerdi	0.246	0.685	0.359	103	0.721
	<b>IDVillenaFemale</b>	<b>-1.646</b>	<b>0.801</b>	<b>-2.054</b>	<b>103</b>	<b>0.043</b>
	IDVillenaMale	-0.184	0.685	-0.268	103	0.789
	<b>SEXMale</b>	<b>-1.434</b>	<b>0.395</b>	<b>-3.633</b>	<b>103</b>	<b>0.000</b>
	YEAR2016	-0.187	0.154	-1.213	103	0.228
	YEAR2017	0.021	0.161	0.133	103	0.894
	YEAR2018	0.096	0.161	0.593	103	0.555
	YEAR2019	0.015	0.168	0.087	103	0.931
	YEAR2020	0.007	0.17	0.042	103	0.966
	YEAR2021	-0.076	0.176	-0.434	103	0.665
K50%	<b>(Intercept)</b>	<b>3.449</b>	<b>0.724</b>	<b>4.764</b>	<b>103</b>	<b>0.000</b>
	IDAdan	0.51	0.372	1.372	103	0.173
	<b>IDAura</b>	<b>-1.279</b>	<b>0.586</b>	<b>-2.184</b>	<b>103</b>	<b>0.031</b>
	IDBerta	-1.19	0.946	-1.259	103	0.211
	IDBlas	-0.177	0.76	-0.232	103	0.817
	IDBoira	-1.934	0.897	-2.155	103	<b>0.033</b>
	IDBoj	0.052	0.824	0.063	103	0.950
	<b>IDBruma</b>	<b>-1.81</b>	<b>0.883</b>	<b>-2.051</b>	<b>103</b>	<b>0.043</b>
	IDCarbo	0.775	0.729	1.063	103	0.290

Value	Variable	Estimate	Std. Error	t val.	d.f.	p-Value
	IDCarla	-0.85	0.875	-0.971	103	0.334
	IDDino	0.187	0.736	0.254	103	0.800
	<b>IDDora</b>	<b>-1.75</b>	<b>0.875</b>	<b>-1.999</b>	<b>103</b>	<b>0.048</b>
	IDEnebro	0.908	0.737	1.233	103	0.220
	IDFaig	0.724	0.734	0.987	103	0.326
	IDFauna	-0.69	0.883	-0.782	103	0.436
	IDFlora	-0.571	0.946	-0.603	103	0.548
	IDGarra	-1.453	0.881	-1.649	103	0.102
	IDGel	0.336	0.734	0.458	103	0.648
	IDHaeckel	-0.095	0.772	-0.123	103	0.902
	IDHelios	-0.015	0.767	-0.019	103	0.985
	<b>IDHydra</b>	<b>-2.16</b>	<b>0.886</b>	<b>-2.438</b>	<b>103</b>	<b>0.017</b>
	IDIris	-1.138	0.903	-1.26	103	0.210
	IDIsis	0.302	0.767	0.394	103	0.695
	IDJara	-1.725	0.883	-1.955	103	0.053
	IDJuan	0.031	0.745	0.042	103	0.966
	IDKarma	-1.23	0.904	-1.361	103	0.176
	IDKoko	0.617	0.772	0.8	103	0.425
	IDLinneo	1.001	0.74	1.352	103	0.179
	IDLucy	-0.567	0.891	-0.636	103	0.526
	IDMargulis	-0.924	0.889	-1.04	103	0.301
	IDMendel	0.701	0.746	0.939	103	0.350
	IDNewton	1.249	0.773	1.615	103	0.109
	IDNube	-0.371	0.947	-0.392	103	0.696
	IDOchoa	0.401	0.746	0.537	103	0.592
	IDOlympia	-1.105	0.889	-1.244	103	0.216
	IDPino	1.382	0.827	1.671	103	0.098
	IDPluma	-1.094	0.9	-1.215	103	0.227
	IDPopper	0.68	0.826	0.822	103	0.413
	IDRosalind	-1.562	0.9	-1.734	103	0.086
	IDRutherford	-0.035	0.757	-0.047	103	0.963
	IDSabina	-1.207	0.915	-1.319	103	0.190

Value	Variable	Estimate	Std. Error	t val.	d.f.	p-Value
	IDSalvia	-0.475	0.917	-0.518	103	0.605
	IDSauce	1.354	0.757	1.789	103	0.077
	IDTaiga	-1.616	0.9	-1.794	103	0.076
	IDTejo	0.063	0.757	0.084	103	0.934
	IDUlex	1.521	0.757	2.009	103	0.047
	IDUva	-0.438	0.915	-0.479	103	0.633
	IDVera	-1.356	0.9	-1.506	103	0.135
	IDVerdi	0.53	0.757	0.7	103	0.485
	<b>IDVillenaFemale</b>	<b>-2.002</b>	<b>0.907</b>	<b>-2.206</b>	<b>103</b>	<b>0.030</b>
	IDVillenaMale	-0.193	0.757	-0.255	103	0.799
	<b>SEXMale</b>	<b>-1.536</b>	<b>0.476</b>	<b>-3.227</b>	<b>103</b>	<b>0.002</b>
	YEAR2016	-0.342	0.186	-1.845	103	0.068
	YEAR2017	-0.078	0.194	-0.404	103	0.687
	YEAR2018	-0.042	0.195	-0.217	103	0.829
	YEAR2019	-0.18	0.202	-0.891	103	0.375
	YEAR2020	-0.196	0.205	-0.954	103	0.342
	YEAR2021	-0.292	0.212	-1.379	103	0.171
Distan	(Intercept)	5.361	3.751	1.429	103	0.156
ca	IDAdan	1.793	0.932	1.923	103	0.057
	IDAura	-0.142	1.468	-0.097	103	0.923
	IDBerta	-2.523	5.213	-0.484	103	0.629
	IDBlas	-1.231	5.019	-0.245	103	0.807
	IDBoira	-2.446	5.159	-0.474	103	0.636
	IDBoj	-0.671	5.082	-0.132	103	0.895
	IDBruma	-2.606	5.143	-0.507	103	0.613
	IDCarbo	-2.785	4.99	-0.558	103	0.578
	IDCarla	-3.402	5.136	-0.662	103	0.509
	IDDino	-1.059	4.997	-0.212	103	0.833
	IDDora	-2.386	5.136	-0.465	103	0.643
	IDEnebro	-1.843	4.997	-0.369	103	0.713
	IDFaig	0.762	4.994	0.153	103	0.879
	IDFauna	-1.009	5.143	-0.196	103	0.845

Value	Variable	Estimate	Std. Error	t val.	d.f.	p-Value
	IDFlora	-0.089	5.214	-0.017	103	0.986
	IDGarra	-4.048	5.142	-0.787	103	0.433
	IDGel	-2.65	4.994	-0.531	103	0.597
	IDHaeckel	-0.41	5.03	-0.081	103	0.935
	IDHelios	-0.974	5.025	-0.194	103	0.847
	IDHydra	-2.359	5.147	-0.458	103	0.648
	IDIris	-2.926	5.165	-0.567	103	0.572
	IDIsis	-1.86	5.025	-0.37	103	0.712
	IDJara	-3.036	5.143	-0.59	103	0.556
	IDJuan	-1.587	5.005	-0.317	103	0.752
	IDKarma	-2.242	5.167	-0.434	103	0.665
	IDKoko	-0.587	5.03	-0.117	103	0.907
	IDLinneo	-2.74	5	-0.548	103	0.585
	IDLucy	-3.949	5.153	-0.766	103	0.445
	IDMargulis	-2.194	5.15	-0.426	103	0.671
	IDMendel	-0.613	5.006	-0.122	103	0.903
	IDNewton	1.647	5.031	0.327	103	0.744
	IDNube	-1.085	5.214	-0.208	103	0.836
	IDOchoa	1.885	5.006	0.377	103	0.707
	IDOlympia	0.653	5.15	0.127	103	0.899
	IDPino	-3.566	5.085	-0.701	103	0.485
	IDPluma	-5.31	5.163	-1.029	103	0.306
	IDPopper	-3.819	5.084	-0.751	103	0.454
	IDRosalind	-4.443	5.163	-0.861	103	0.391
	IDRutherford	-3.043	5.016	-0.607	103	0.545
	IDSabina	-2.368	5.179	-0.457	103	0.648
	IDSalvia	-1.304	5.181	-0.252	103	0.802
	IDSauce	0.022	5.016	0.004	103	0.997
	IDTaiga	-3.44	5.163	-0.666	103	0.507
	IDTejo	-2.098	5.016	-0.418	103	0.677
	IDUlex	5.47	5.016	1.091	103	0.278
	IDUva	2.074	5.179	0.401	103	0.690

Value	Variable	Estimate	Std. Error	t val.	d.f.	p-Value
	IDVera	-2.634	5.163	-0.51	103	0.611
	IDVerdi	-1.074	5.016	-0.214	103	0.831
	IDVillenaFemale	-0.733	5.171	-0.142	103	0.888
	IDVillenaMale	-0.334	5.016	-0.067	103	0.947
	SEXMale	-1.379	1.194	-1.155	103	0.251
	YEAR2016	0.161	0.465	0.347	103	0.729
	YEAR2017	-0.027	0.486	-0.056	103	0.956
	YEAR2018	0.283	0.488	0.58	103	0.563
	YEAR2019	0.421	0.507	0.831	103	0.408
	YEAR2020	0.368	0.514	0.716	103	0.476
	YEAR2021	1.042	0.531	1.962	103	0.053

**Table S3** Inter-annual overlap percentages of territory A's individuals.

	Abel 2015	Abel 2016	Adan 2017	Adan 2018	Adan 2019	Adan 2020	Aura 2015	Aura 2016	Aura 2017	Aura 2018	Aura 2019	Aura 2020	Aura 2021
Abel2015	1.000	0.778	0.771	0.775	0.645	0.647	0.955	0.816	0.744	0.648	0.603	0.683	0.628
Abel2016	0.861	1.000	0.892	0.937	0.764	0.767	0.876	0.946	0.866	0.771	0.701	0.812	0.704
Adan2017	0.870	0.910	1.000	0.926	0.730	0.752	0.878	0.917	0.918	0.732	0.661	0.779	0.685
Adan2018	0.453	0.495	0.480	1.000	0.780	0.703	0.452	0.479	0.457	0.884	0.731	0.802	0.686
Adan2019	0.469	0.501	0.470	0.969	1.000	0.847	0.473	0.491	0.463	0.946	0.925	0.953	0.872
Adan2020	0.528	0.565	0.543	0.980	0.950	1.000	0.528	0.558	0.525	0.917	0.903	0.950	0.902
Aura2015	0.958	0.795	0.781	0.775	0.653	0.650	1.000	0.829	0.749	0.648	0.611	0.690	0.639
Aura2016	0.871	0.912	0.867	0.874	0.721	0.731	0.881	1.000	0.860	0.731	0.666	0.767	0.677
Aura2017	0.888	0.933	0.970	0.931	0.759	0.768	0.890	0.961	1.000	0.775	0.693	0.807	0.707
Aura2018	0.411	0.442	0.412	0.960	0.827	0.714	0.410	0.435	0.412	1.000	0.805	0.853	0.748
Aura2019	0.460	0.484	0.447	0.955	0.972	0.846	0.465	0.477	0.443	0.969	1.000	0.959	0.899
Aura2020	0.474	0.509	0.479	0.951	0.909	0.808	0.477	0.499	0.469	0.932	0.871	1.000	0.850
Aura2021	0.462	0.468	0.446	0.862	0.882	0.813	0.468	0.466	0.436	0.866	0.866	0.901	1.000

**Table S4** Inter-annual overlap percentages of territory B's individuals.

	Berta 2015	Blas 2015	Blas 2016	Boira 2015	Boira 2016	Boj 2017	Bruma 2017	Bruma 2018	Bruma 2019	Bruma 2020	Bruma 2021
Berta2015	1.000	0.835	0.608	0.665	0.564	0.632	0.646	0.797	0.641	0.709	0.548
Blas2015	0.759	1.000	0.604	0.718	0.555	0.584	0.659	0.783	0.625	0.716	0.526
Blas2016	0.859	0.938	1.000	0.908	0.833	0.843	0.922	0.980	0.867	0.975	0.805
Boira2015	0.635	0.755	0.614	1.000	0.549	0.580	0.635	0.754	0.569	0.705	0.544
Boira2016	0.881	0.953	0.921	0.897	1.000	0.840	0.897	0.929	0.858	0.945	0.818
Boj2017	0.917	0.930	0.865	0.880	0.780	1.000	0.942	0.996	0.879	0.969	0.771
Bruma2017	0.768	0.861	0.776	0.789	0.683	0.772	1.000	0.977	0.819	0.884	0.689
Bruma2018	0.639	0.690	0.556	0.632	0.477	0.550	0.659	1.000	0.586	0.682	0.472
Bruma2019	0.874	0.937	0.837	0.812	0.749	0.828	0.941	0.998	1.000	0.952	0.754
Bruma2020	0.773	0.859	0.753	0.804	0.660	0.729	0.811	0.928	0.761	1.000	0.669
Bruma2021	0.892	0.941	0.927	0.926	0.853	0.866	0.943	0.958	0.899	0.999	1.000

**Table S5** Inter-annual overlap percentages of territory C's individuals.

	Carbo 2015	Carbo 2016	Carbo 2017	Carbo 2018	Carbo 2019	Carbo 2020	Carla 2015	Carla 2016	Carla 2017	Carla 2018
Carbo2015	1.000	0.852	0.861	0.801	0.756	0.719	0.879	0.825	0.839	0.815
Carbo2016	0.660	1.000	0.895	0.836	0.772	0.689	0.609	0.630	0.879	0.859
Carbo2017	0.628	0.842	1.000	0.788	0.745	0.689	0.576	0.617	0.945	0.834
Carbo2018	0.676	0.912	0.912	1.000	0.838	0.734	0.623	0.640	0.894	0.966
Carbo2019	0.692	0.912	0.935	0.908	1.000	0.799	0.632	0.666	0.912	0.949
Carbo2020	0.674	0.833	0.886	0.814	0.819	1.000	0.644	0.709	0.855	0.823
Carla2015	0.947	0.847	0.851	0.795	0.744	0.741	1.000	0.837	0.830	0.802
Carla2016	0.769	0.757	0.788	0.706	0.678	0.705	0.724	1.000	0.782	0.721
Carla2017	0.611	0.826	0.943	0.771	0.726	0.664	0.561	0.611	1.000	0.819
Carla2018	0.620	0.843	0.870	0.870	0.789	0.668	0.566	0.588	0.855	1.000



**Table S6** Inter-annual overlap percentages of territory D's individuals.

	Dino2015	Dino2016	Dino2017	Dino2018	Dora2015	Dora2016	Dora2017	Dora2018
Dino2015	1.000	0.869	0.880	0.987	0.984	0.784	0.817	0.987
Dino2016	0.895	1.000	0.940	0.960	0.897	0.848	0.866	0.960
Dino2017	0.843	0.874	1.000	0.991	0.855	0.783	0.899	0.991
Dino2018	0.712	0.672	0.746	1.000	0.725	0.588	0.678	0.984
Dora2015	0.962	0.851	0.873	0.983	1.000	0.768	0.809	0.982
Dora2016	0.951	0.999	0.991	0.989	0.954	1.000	0.956	0.990
Dora2017	0.865	0.890	0.993	0.994	0.876	0.834	1.000	0.994
Dora2018	0.719	0.679	0.754	0.994	0.733	0.595	0.685	1.000

**Table S7** Inter-annual overlap percentages of territory E's individuals.

	Enebro2016	Enebro2017	Enebro2018	Enebro2019	Enebro2020
Enebro2016	1.000	0.859	0.766	0.829	0.772
Enebro2017	0.789	1.000	0.723	0.841	0.736
Enebro2018	0.913	0.939	1.000	0.935	0.862
Enebro2019	0.819	0.904	0.774	1.000	0.809
Enebro2020	0.880	0.915	0.825	0.935	1.000

**Table S8** Inter-annual overlap percentages of territory F's individuals.

	Faig 2016	Faig 2017	Faig 2018	Faig2 019	Faig 2020	Faig 2021	Flora 2016	Fauna 2017	Fauna 2018	Fauna 2019	Fauna 2020	Fauna 2021
Faig2016	1.000	0.928	0.914	0.908	0.947	0.934	0.984	0.968	0.963	0.922	0.946	0.980
Faig2017	0.785	1.000	0.838	0.798	0.890	0.856	0.813	0.979	0.913	0.851	0.886	0.940
Faig2018	0.858	0.930	1.000	0.918	0.942	0.913	0.883	0.961	0.995	0.950	0.941	0.971
Faig2019	0.851	0.883	0.916	1.000	0.955	0.901	0.877	0.942	0.970	0.994	0.960	0.967
Faig2020	0.815	0.904	0.863	0.877	1.000	0.853	0.850	0.957	0.919	0.911	0.961	0.933
Faig2021	0.764	0.827	0.795	0.786	0.810	1.000	0.796	0.928	0.890	0.824	0.834	1.000
Flora2016	0.906	0.885	0.866	0.862	0.910	0.897	1.000	0.930	0.917	0.877	0.913	0.949
Fauna2017	0.708	0.847	0.749	0.736	0.814	0.831	0.739	1.000	0.854	0.789	0.825	0.941
Fauna2018	0.770	0.863	0.848	0.828	0.855	0.872	0.797	0.934	1.000	0.884	0.871	0.965
Fauna2019	0.786	0.857	0.863	0.905	0.903	0.860	0.813	0.919	0.942	1.000	0.921	0.950
Fauna2020	0.794	0.879	0.842	0.861	0.938	0.857	0.833	0.946	0.914	0.907	1.000	0.940
Fauna2021	0.622	0.705	0.657	0.656	0.689	0.777	0.655	0.816	0.766	0.708	0.711	1.000

**Table S9** Inter-annual overlap percentages of territory G's individuals.

	Gel 2016	Gel 2017	Gel 2018	Gel 2019	Gel 2020	Gel 2021	Garra 2016	Garra 2017	Garra 2018	Garra 2019
Gel2016	1.000	0.936	0.881	0.913	0.829	0.748	0.939	0.898	0.854	0.797
Gel2017	0.582	1.000	0.907	0.932	0.876	0.701	0.549	0.894	0.862	0.726
Gel2018	0.527	0.872	1.000	0.907	0.888	0.681	0.498	0.814	0.908	0.715
Gel2019	0.543	0.891	0.902	1.000	0.900	0.687	0.513	0.825	0.835	0.732
Gel2020	0.525	0.891	0.939	0.956	1.000	0.719	0.497	0.829	0.885	0.749
Gel2021	0.605	0.911	0.920	0.933	0.919	1.000	0.579	0.846	0.862	0.854
Garra2016	0.998	0.938	0.885	0.917	0.836	0.761	1.000	0.903	0.861	0.811
Garra2017	0.618	0.990	0.937	0.953	0.901	0.720	0.585	1.000	0.913	0.749
Garra2018	0.558	0.905	0.991	0.916	0.913	0.697	0.529	0.866	1.000	0.723
Garra2019	0.599	0.876	0.897	0.924	0.889	0.794	0.573	0.817	0.831	1.000

**Table S10** Inter-annual overlap percentages of territory H's individuals.

	Helios2016	Helios2017	Haeckel2017	Haeckel2018	Hydra2016	Hydra2017	Hydra2018
Helios2016	1.000	0.918	0.951	0.957	0.964	0.929	0.640
Helios2017	0.874	1.000	0.943	0.950	0.848	0.915	0.592
Haeckel2017	0.634	0.661	1.000	0.762	0.617	0.758	0.432
Haeckel2018	0.749	0.782	0.896	1.000	0.729	0.839	0.508
Hydra2016	0.973	0.900	0.935	0.940	1.000	0.913	0.631
Hydra2017	0.817	0.845	0.999	0.941	0.794	1.000	0.565
Hydra2018	0.988	0.959	1.000	1.000	0.964	0.991	1.000

**Table S11** Inter-annual overlap percentages of territory I's individuals.

	Isis2016	Isis2017	Iris2016	Iris2017
Isis2016	1.000	0.710	0.877	0.763
Isis2017	0.840	1.000	0.827	0.894
Iris2016	0.896	0.714	1.000	0.795
Iris2017	0.626	0.621	0.639	1.000

**Table S12** Inter-annual overlap percentages of territory J's individuals.

	Juan 2017	Juan 2018	Juan 2019	Juan 2020	Jara 2017	Jara 2018	Jara 2019	Jara 2020	Jara 2021
Juan2017	1.000	0.758	0.758	0.600	0.650	0.850	0.692	0.472	0.337
Juan2018	0.905	1.000	1.000	0.710	0.752	0.838	0.889	0.563	0.402
Juan2019	0.905	1.000	1.000	0.710	0.752	0.838	0.889	0.563	0.402
Juan2020	0.935	0.928	0.928	1.000	0.836	0.912	0.889	0.743	0.525
Jara2017	0.961	0.931	0.931	0.792	1.000	0.906	0.921	0.667	0.492
Jara2018	0.991	0.819	0.819	0.682	0.715	1.000	0.769	0.547	0.393
Jara2019	0.926	0.997	0.997	0.762	0.833	0.881	1.000	0.619	0.449
Jara2020	0.992	0.991	0.991	0.999	0.947	0.985	0.971	1.000	0.691
Jara2021	1.000	1.000	1.000	0.998	0.986	0.998	0.995	0.976	1.000

**Table S13** Inter-annual overlap percentages of territory K's individuals.

	Koko2017	Koko2018	Karma2017	Karma2018
Koko2017	1.000	0.812	0.965	0.739
Koko2018	0.577	1.000	0.598	0.740
Karma2017	0.772	0.674	1.000	0.609
Karma2018	0.705	0.995	0.727	1.000

**Table S14** Inter-annual overlap percentages of territory L's individuals.

	Linneo 2017	Linneo 2018	Linneo 2019	Linneo 2020	Linneo 2021	Linneo 2017	Linneo 2018	Lucy 2019
Linneo2017	1.000	0.791	0.687	0.796	0.682	0.925	0.803	0.748
Linneo2018	0.870	1.000	0.848	0.911	0.821	0.837	0.929	0.893
Linneo2019	0.846	0.949	1.000	0.969	0.919	0.814	0.917	0.997
Linneo2020	0.839	0.873	0.831	1.000	0.826	0.807	0.846	0.895
Linneo2021	0.807	0.883	0.884	0.926	1.000	0.765	0.847	0.961
Linneo2017	0.987	0.812	0.707	0.817	0.691	1.000	0.825	0.763
Linneo2018	0.907	0.954	0.842	0.906	0.809	0.873	1.000	0.878
Lucy2019	0.808	0.877	0.875	0.917	0.878	0.773	0.840	1.000

**Table S15** Inter-annual overlap percentages of territory M's individuals.

	Mendel 2018	Mendel 2019	Mendel 2020	Mendel 2021	Margulis 2018	Margulis 2019	Margulis 2020	Margulis 2021
Mendel2018	1.000	0.911	0.920	0.819	0.954	0.935	0.938	0.697
Mendel2019	0.879	1.000	0.921	0.816	0.861	0.959	0.902	0.691
Mendel2020	0.889	0.921	1.000	0.793	0.885	0.930	0.964	0.679
Mendel2021	0.827	0.852	0.828	1.000	0.815	0.845	0.815	0.757
Margulis2018	0.964	0.901	0.926	0.816	1.000	0.929	0.946	0.697
Margulis2019	0.873	0.927	0.899	0.782	0.859	1.000	0.899	0.683
Margulis2020	0.904	0.900	0.961	0.778	0.901	0.928	1.000	0.676
Margulis2021	0.888	0.910	0.895	0.955	0.878	0.931	0.893	1.000

**Table S16** Inter-annual overlap percentages of territory N's individuals.

	Newton2018	Newton2019	Nube2018
Newton2018	1.000	0.807	0.896
Newton2019	0.810	1.000	0.816
Nube2018	0.915	0.830	1.000

**Table S17** Inter-annual overlap percentages of territory O's individuals.

	Ochoa 2018	Ochoa 2019	Ochoa 2020	Ochoa 2021	Olympia 2018	Olympia 2019	Olympia 2020	Olympia 2021
Ochoa2018	1.000	0.894	0.945	0.985	0.916	0.864	0.990	0.973
Ochoa2019	0.933	1.000	0.985	1.000	0.890	0.942	1.000	1.000
Ochoa2020	0.487	0.486	1.000	0.808	0.467	0.472	0.933	0.738
Ochoa2021	0.465	0.452	0.740	1.000	0.440	0.435	0.839	0.755
Olympia2018	0.978	0.910	0.969	0.997	1.000	0.879	0.993	0.991
Olympia2019	0.936	0.978	0.993	0.999	0.892	1.000	0.999	0.999
Olympia2020	0.365	0.353	0.668	0.656	0.343	0.340	1.000	0.608
Olympia2021	0.487	0.480	0.717	0.801	0.465	0.461	0.826	1.000

**Table S18** Inter-annual overlap percentages of territory P's individuals.

	Popper2019	Pino2020	Pluma2019	Pluma2020	Pluma2021
Popper2019	1.000	0.972	0.889	0.926	0.636
Pino2020	0.748	1.000	0.682	0.768	0.506
Pluma2019	0.983	0.979	1.000	0.935	0.646
Pluma2020	0.927	0.999	0.847	1.000	0.654
Pluma2021	0.963	0.996	0.884	0.989	1.000

**Table S19** Inter-annual overlap percentages of territory R's individuals.

	Rutherford 2019	Rutherford 2020	Rutherford 2021	Rosalind 2019	Rosalind 2020	Rosalind 2021
Rutherford2019	1.000	0.930	0.915	0.976	0.958	0.902
Rutherford2020	0.940	1.000	0.950	0.951	0.992	0.943
Rutherford2021	0.829	0.852	1.000	0.828	0.874	0.939
Rosalind2019	0.953	0.918	0.891	1.000	0.948	0.884
Rosalind2020	0.916	0.938	0.922	0.928	1.000	0.911
Rosalind2021	0.824	0.852	0.946	0.827	0.871	1.000

**Table S20** Inter-annual overlap percentages of territory S's individuals.

	Sauce 2019	Sauce 2020	Sauce 2021	Sabina 2019	Sabina 2020	Salvia 2020	Salvia 2021
Sauce2019	1.000	0.932	0.671	0.953	0.303	0.993	0.581
Sauce2020	0.837	1.000	0.672	0.825	0.272	1.000	0.576
Sauce2021	0.849	0.947	1.000	0.850	0.374	0.998	0.815
Sabina2019	0.955	0.920	0.673	1.000	0.303	0.994	0.582
Sabina2020	1.000	1.000	0.974	1.000	1.000	1.000	0.889
Salvia2020	0.583	0.654	0.463	0.582	0.178	1.000	0.402
Salvia2021	0.847	0.936	0.939	0.846	0.392	0.999	1.000

**Table S21** Inter-annual overlap percentages of territory T's individuals.

	Tejo2019	Tejo2020	Tejo2021	Taiga2019	Taiga2020	Taiga2021
Tejo2019	1.000	0.996	0.781	0.988	0.988	0.836
Tejo2020	0.797	1.000	0.729	0.917	0.978	0.756
Tejo2021	0.832	0.970	1.000	0.920	0.967	0.931
Taiga2019	0.834	0.968	0.729	1.000	0.973	0.771
Taiga2020	0.787	0.974	0.723	0.918	1.000	0.750
Taiga2021	0.814	0.921	0.852	0.890	0.917	1.000

**Table S22** Inter-annual overlap percentages of territory U's individuals.

	Ulex2019	Ulex2020	Uva2019	Uva2020
Ulex2019	1.000	0.548	0.997	0.407
Ulex2020	0.885	1.000	0.929	0.708
Uva2019	0.721	0.416	1.000	0.314
Uva2020	0.862	0.930	0.922	1.000

**Table S23** Inter-annual overlap percentages of territory V's individuals.

	Verdi2019	Verdi2020	Verdi2021	Vera2019	Vera2020	Vera2021
Verdi2019	1.000	0.996	0.743	0.921	0.932	0.701
Verdi2020	0.638	1.000	0.545	0.614	0.837	0.462
Verdi2021	0.873	1.000	1.000	0.872	0.970	0.774
Vera2019	0.960	1.000	0.774	1.000	0.982	0.724
Vera2020	0.706	0.990	0.626	0.713	1.000	0.543
Vera2021	0.974	1.000	0.914	0.964	0.995	1.000

**Table S24** Inter-annual overlap percentages of territory W's individuals.

	VillenaMale 2018	VillenaMale 2019	VillenaMale 2020	VillenaMale 2021	VillenaFemale 2018	VillenaFemale 2019
VillenaMale2018	1.000	0.442	0.477	0.389	0.424	0.381
VillenaMale2019	0.969	1.000	0.808	0.687	0.793	0.832
VillenaMale2020	0.989	0.764	1.000	0.616	0.723	0.679
VillenaMale2021	0.891	0.718	0.681	1.000	0.604	0.587
VillenaFemale2018	1.000	0.854	0.823	0.622	1.000	0.802
VillenaFemale2019	0.957	0.954	0.823	0.644	0.853	1.000

**Table S25** Overlap percentages of A territory (original territory) compared with the previous year (2017) before the death of D territorial pair (Dino and Dora) and overlap percentages of the new territory occupied (D) by the A territorial pair.

Individual	Year	Overlap % 2017's comparing home- range	Overlap % of occupied Dino 2018's home-range	Overlap % of occupied Dora 2018's home-range
Aura	2018	77.5	77.15	77.45
Adan	2018	92.6	77.03	75.42
Aura	2019	69.3	60.75	61.02
Adan	2019	73.2	62.14	62.31
Aura	2020	80.7	62.11	62.30
Adan	2020	75.2	50.66	50.72
Aura	2021	70.7	53.84	53.74





**Figure S1** Annual home-range representation of each individual. The K95%, K75% and K50% are observed such as three isopleths (from the outside in), the centroid of K95% in red and the nest in blue. We can see the stability during the years and the different territorial owners.



**Table S26** Distances between centroids and nest. The annual eccentricity of each individual.

ID.YEAR	Distance (m)	ID.YEAR	Distance (m)	ID.YEAR	Distance (m)	ID.YEAR	Distance (m)
Abel2015	3639.59	Dora2017	2981.35	Jara2017	2085.21	Pino2020	784.53
Abel2016	4486.53	Dora2018	3007.79	Jara2018	2755.53	Pluma2019	833.97
Adan2017	4653.88	Enebro2016	2015.86	Jara2019	2496.37	Pluma2020	417.88
Adan2018	6400.46	Enebro2017	2296.89	Jara2020	3165.16	Pluma2021	733.16
Adan2019	6526.10	Enebro2019	2653.34	Jara2021	3213.71	Popper2019	584.12
Adan2020	6565.83	Enebro2020	2230.39	Juan2017	2057.76	Rosalind2019	1207.41
Aura2015	3550.72	Enebro2028	2704.65	Juan2018	2643.92	Rosalind2020	1412.75
Aura2016	4325.02	Faig2016	5678.88	Juan2019	2602.71	Rosalind2021	1966.42
Aura2017	4684.35	Faig2017	5255.06	Juan2020	3320.56	Rutherford2019	1289.01
Aura2018	6695.32	Faig2018	5040.11	Karma2017	2539.81	Rutherford2020	1480.94
Aura2019	6406.83	Faig2019	4576.88	Karma2018	3954.36	Rutherford2021	1879.28
Aura2020	6537.32	Faig2020	4530.62	Koko2017	2215.79	Sabina2019	4307.66
Aura2021	6586.28	Faig2021	5631.71	Koko2018	4829.86	Sabina2020	2467.51
Berta2015	2838.00	Fauna2017	5030.71	Linne02017	1221.24	Salvia2020	5363.06
Blas2015	2294.33	Fauna2018	4831.83	Linne02018	1821.77	Salvia2021	4162.81
Blas2016	3370.07	Fauna2019	4265.31	Linne02019	1667.03	Sauce2019	4489.72
Boira2015	2683.33	Fauna2020	4462.04	Linne02020	1727.11	Sauce2020	5207.18
Boira2016	3307.80	Fauna2021	5260.91	Linne02021	1862.68	Sauce2021	4147.86
Boj2017	3283.96	Flora2016	5434.24	Lucy2017	1359.39	Taiga2019	2267.40
Bruma2017	3310.81	Garra2016	1048.50	Lucy2018	1730.40	Taiga2020	2310.50
Bruma2018	2902.53	Garra2017	1829.92	Lucy2019	1823.18	Taiga2021	3016.63
Bruma2019	3292.42	Garra2018	2215.63	Margulis2018	3540.18	Tejo2019	2321.28
Bruma2020	3282.21	Garra2019	996.33	Margulis2019	3581.43	Tejo2020	2287.56
Bruma2021	3077.05	Gel2016	1057.16	Margulis2020	3541.23	Tejo2021	2875.75
Carbo2015	2582.22	Gel2017	1767.76	Margulis2021	4119.40	Ulex2019	9574.16
Carbo2016	1086.94	Gel2018	2288.47	Mendel2018	3754.30	Ulex2020	6323.07
Carbo2017	1560.64	Gel2019	1700.82	Mendel2019	3713.83	Ulex2021	14292.83
Carbo2018	908.85	Gel2020	1842.51	Mendel2020	3552.56	Uva2019	11197.23
Carbo2019	743.22	Gel2021	1585.16	Mendel2021	4573.10	Uva2020	4463.06
Carbo2020	1511.67	Haeckel2017	4073.14	Newton2018	5263.87	Vera2019	3753.95
Carla2015	2606.37	Haeckel2018	3328.06	Newton2019	6698.60	Vera2020	3113.73
Carla2016	2774.27	Helios2016	3009.82	Nube2018	4559.72	Vera2021	3147.42
Carla2017	1772.43	Helios2017	3140.75	Ochoa2018	5032.14	Verdi2019	4198.47
Carla2018	1100.17	Hydra2016	2941.28	Ochoa2019	4666.57	Verdi2020	3254.14
Dino2015	3243.72	Hydra2017	3533.54	Ochoa2020	7682.48	Verdi2021	3104.43
Dino2016	2859.00	Hydra2018	2948.19	Ochoa2021	8204.01	VillFemale2018	5543.73
Dino2017	2973.32	Iris2016	2667.96	Olympia2018	4959.44	VillFemale2019	4417.61
Dino2018	3033.89	Iris2017	2336.67	Olympia2019	4762.40	VillMale2018	5310.40
Dora2015	3322.80	Isis2016	2967.32	Olympia2020	7904.76	VillMale2019	4213.34
Dora2016	3005.16	Isis2017	1411.53	Olympia2021	8546.17	VillMale2020	4713.12
						VillMale2021	3850.40

